

















# ILLINOIS BIOLOGICAL MONOGRAPHS

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EDITORIAL COMMITTEE

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STEPHEN ALFRED FORBES

WILLIAM TRELEASE

HENRY BALDWIN WARD





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ILLINOIS BIOLOGICAL  
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# STUDIES ON GREGARINES II

SYNOPSIS OF THE POLYCYSTID GREGARINES  
OF THE WORLD, EXCLUDING THOSE  
FROM THE MYRIAPODA,  
ORTHOPTERA, AND  
COLEOPTERA

WITH FOUR PLATES

BY

MINNIE WATSON KAMM

Contributions from the  
Zoological Laboratory of the University of Illinois  
under the direction of Henry B. Ward, No. 195





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## INTRODUCTION

This monograph constitutes the second half of a problem in which it is endeavored to bring together in small compass the more important facts concerning the systematic position of polycystid gregarines. The first part of the work (Watson, 1916a) was published in 1916 and included the polycystid gregarines recorded from the Coleoptera, Orthoptera, and Myriapoda of the world. The present paper comprises those from the remainder of the animal kingdom. It is designed chiefly for the use of workers on gregarines who do not have access to the vast literature which has developed upon the subject and with which the University library is so richly endowed.

I wish to thank Professor Henry Baldwin Ward for kindly encouraging the publication of this paper, for his advice and judgment concerning some of the knotty systematic questions involved, and for the use of the laboratory and library facilities in his Department.

When the first paper was published Dr. C. W. Stiles, of Washington, informed me concerning the desirability of designating the type species of the various genera, and this has been done in the present paper. He also gave his opinion concerning the type species of the genus *Cephaloidophora*, for which I wish to express my thanks.

The larger groupings used in the present paper are made from the standpoint of the host-material rather than the parasite itself in order to facilitate work in the field. From the descriptions it can be at once determined whether or not a particular gregarine has ever been found in identical or similar material. If it has not been described from hosts in the same group and its position is definitely established from some one or more of the generic characters, one may turn to the index of this and of the preceding paper, where all the known species in each genus are ranged in alphabetical order under the generic name. From a comparison of all the known species with the species in hand it may be determined whether or not the latter has been described from some other group. It is true, however, that except in rare instances a species is confined to a single host or to nearly-related hosts, not being found in insects as far removed from each other as the Coleoptera and the Orthoptera.

In this paper I have not tabulated a complete alphabetic list of the gregarine genera with their hosts or of the hosts with their parasites for this reason: Two such lists were given in the former paper covering the species

up to 1915, and those described since then are listed in the same manner at the end of the present paper.

The previous monograph covers the species known from the Coleoptera, Orthoptera, and Myriapoda up to the year 1915. The gregarines parasitic in the remainder of the animal kingdom up to the beginning of 1920 are described in the present work. The arrangement of hosts in orders and classes of the Hexapoda follows that given by Comstock (1912).

Because more and more species are being described in such great genera as *Gregarina*, *Actinocephalus*, etc., which are very similar in all their characteristics but yet are distinct species, I believe accurate and detailed measurements are necessary for the sporonts, trophozoites, cysts, and spores, or as many of these characters as may be determined. Measurements should be made of quiescent but not water-swollen animals while alive on the slide. These measurements must needs be made very quickly after the host is opened for a water medium is highly destructive to the ectosarc of the gregarine, at first causing it to swell out of all normal proportions and then to break, with the collapse of the animal. When the parasites do not die within a short time (e.g., the *Stenophoridae*) they at least lose their original proportions and measurements become valueless. Those taken on preserved material are far from accurate.

Ratios used in this paper indicate length of protomerite to total length (LP:TL) and width of protomerite to width of deutomerite (WP:WD) as indicated in the author's drawings even though no measurements may have been made.

One would like to make a clean-cut and sweeping statement that polycystid gregarines are parasites of the arthropods exclusively and unless an exhaustive study be made this may seem to be true.

But just as higher animals cannot be placed under such definite groups, so it is with these simply organized forms. There is a gradual transition from simple to complex—from the unilocular to the septate forms, and from the simpler to the higher septate organisms. As shown in the group of tables in this paper, I believe there is an interesting and not entirely imaginary parallelism in the character of the hosts which harbor these developing parasites. The transitional forms between non-septate and septate gregarines are found exclusively in the polychaetes. The two lowest (and very similar) families of septate gregarines are found in lowly organized arthropods—the Crustacea and Diplopoda. These gregarines possess no epimerites or very rudimentary ones.

The next higher family, in which the epimerite is a very simple structure, is abundantly represented in the Orthoptera, but also in the Coleoptera (which is not one of the lower orders), and is fairly general throughout the Hexapoda. Just as the line of evolution in higher animals may take a single track however aberrant it may prove to be, this is apparently



true in gregarines, for many instances may be mentioned in which genera are found exclusively in a single order of insects; the genus most frequently present in the Acerata (Sciadophora) is found nowhere else and is highly specialized and unique along a particular line.

A gregarine has even been found in *Peripatus*; and the Tunicates contain true septate forms. It would be interesting to know what becomes of these parasites above the Tunicates—whether they lose their gregarinoid and take on higher characteristics, continuing to develop in vertebrates, or whether the alimentary tract of the latter contain enzymes not suited to their continued existence and they are thereby extinguished.

A suggested problem is that of the possibility of the existence of gregarines in the insects found in Baltic amber; the insects being transparent their presence or absence should be easily determined, and possibly some of the generic characters.

## CLASSIFICATION OF THE TRIBE CEPHALINA

## WITH THE TYPE SPECIES

## Order 1. Gregarinoidea Minchin 1912.

## Suborder 1. Eugregarinae Léger 1900.

## Tribe 1. Cephalina Delage and Hérourard 1896 (Intestinal parasites almost exclusively).

Family 1. Lecudinidae Kamm 1922. Non-septate gregarines inhabiting digestive tract of polychaetes. Epimerite a simple knob.

Genus 1. *Lecudina* Mingazzini 1891:469. Non-septate, epimerite simple, spores ovoidal with thickening at one pole.

Type: *Lecudina pellucida* (Köl liker) Mingazzini.

Family 2. Polyrrhabdinidae Kamm 1922. Septate gregarines inhabiting the digestive tract of polychaetes. Epimerites varied.

Genus 2. *Polyrrhabdina* Mingazzini 1891:229. Septate, sporonts flattened, ovoidal, epimerite a corona of hooks. Intestine of polychaetes of the family Spionidae.

Type species: *Polyrrhabdina spionis* (Köll.) Ming.

Genus 3. *Sycia* Léger 1892:52. Epimerite knobbed, bordered by a thick ring. Protomerite subspherical, deutomerite conical with many inclosures in adult.

Type: *Sycia inopinata* Léger.

Genus 4. *Ulivina* Mingazzini 1891:235. Elongate-ellipsoidal, protomerite the more dense.

Type: *Ulivina elliptica* Ming.

Family 3. Cephaloidophoridae Kamm 1922. Sporonts associated in twos, no epimerite. Development intracellular; cyst dehiscence by simple rupture, spores ovoidal with equatorial line. Parasites of Crustacea.

Genus 5. *Cephaloidophora* Mawrodiadi 1908:101. Characters of the family.

Type: *Cephaloidophora communis* Mawrodiadi.

Family 4. Stenophoridae Léger and Duboscq 1904:361. Sporonts solitary, epimerite absent or rudimentary. Development intracellular; cyst dehiscence by simple rupture, spores ovoidal with equatorial line. Confined to Diplopods.

Genus 6. *Stenophora* Labbé 1899:15. Characters of the family.

Type: *Stenophora juli* (Frantz.) Schn.

Genus 7. *Fonsecaia* Pinto 1918: ? Like type genus except spores elongate-ellipsoidal, no endospore.

Type: *Fonsecaia polymorpha* Pinto.

Family 5. Gregarinidae Labbé 1899:9. Epimerite symmetrical, simple. Sporonts solitary or in association. Cysts with or without spore-ducts, spores symmetrical. (Confined to insects with two exceptions, development extracellular.)

Genus 8. *Leidyana* Watson 1915:35. Sporonts solitary, epimerite a simple sessile knob. Dehiscence by spore-ducts. Spores barrel-shaped, in chains.

Type: *Leidyana erratica* (Crawl.) Wats.

Remarks in parenthesis are added by the writer.

- Genus 9. *Gregarina* Dufour 1828:366. Sporonts associated in twos, epimerite a simple globular or cylindrical papilla. Cysts with spore-ducts, spores barrel-shaped, extruded in chains.

Type: *Gregarina ovata* Duf.

- Genus 10. *Protomagalhãensia* Pinto 1918: ? Sporonts in associations of several individuals, often attached laterally. Myonemes prominent. Sporonts attenuate. (Cysts and epimerites unknown.) Spores barrel-shaped, spine at each corner.

Type: *Protomagalhãensia serpentula* (Magal.) Pinto.

- Genus 11. *Gamocystis* Schneider 1875:587. Protomerite only in trophozoite, sporonts in twos; sporulation partial, with spore-ducts, spores cylindrical.

Type: *Gamocystis tenax* Schn.

- Genus 12. *Hyalospora* Schneider 1875:583. Sporonts in associations of two, endoplasm yellow-orange. Epimerite a simple globular knob. Cyst dehiscence by simple rupture, spores ellipsoidal.

Type: *Hyalospora roscoviana* Schn.

- Genus 13. *Hirmocystis* Labbé 1899:12. Sporonts in associations of from two to twelve (or more). Epimerite a small cylindrical papilla. Cysts spherical, dehiscence by simple rupture, spores ovoidal.

Type: *Hirmocystis ventricosa* (Léger) Labbé.

- Genus 14. *Euspora* Schneider 1875:582. Sporonts in twos. (Epimerite unknown.) Cysts spherical, dehiscence by simple rupture, spores prismatic.

Type: *Euspora fallax* Schn.

- Genus 15. *Sphaerocystis* Léger 1892:115. Protomerite only in trophic stages, sporonts solitary, subspherical. Cysts spherical, dehiscence by simple rupture, spores ovoidal.

Type: *Sphaerocystis simplex* Léger.

- Genus 16. *Cnemidospora* Schneider 1882:446. Sporonts solitary, anterior half of protomerite gray, posterior half yellow-green. (Epimerite not known.) Cyst dehiscence by simple rupture, spores ellipsoidal.

Type: *Cnemidospora lutea* Schn.

- Genus 17. *Uradiophora* Mercier 1912:198. Sporonts in twos, deutomerite with small appendix. Epimerite an elongate papilla. Cysts ovoidal, dehiscence by simple rupture, spores spherical or subspherical, extruded in chains. Development extra-cellular.

Type: *Uradiophora cuenoti* (Merc.) Merc.

- Genus 18. *Pyxinoides* Trégouboff 1921: liii. Sporonts in associations of two, epimerite a slightly stalked globular papilla with sixteen longitudinal furrows, small cone at apex. Extra-cellular development.

Type: *Pyxinoides balani* (Köll.) Trég.



Family 6. Didymophyidae Léger 1892:105. Sporonts in associations of two or three. No septum in satellites.

Genus 19. Didymophyes Stein 1848:186. Epimerite a small pointed papilla. Cysts spherical, dehiscence by simple rupture, spores ellipsoidal.

Type: *Didymophyes gigantea* Stein.

Family 7. Actinocephalidae Léger 1892:166. Sporonts solitary, epimerites complex and varied. Cyst dehiscence by simple rupture, spores irregular, biconical, or cylindro-biconical. (Practically confined to insects.)

Genus 20. Amphoroides Labbé 1899:20. Protomerite cup-shaped, epimerite a globular sessile papilla. Spores curved.

Type: *Amphoroides polydesmi* (Léger) Labbé.

Genus 21. Pileocephalus Schneider 1875:591. Epimerite a lance-shaped cone on a short neck. Spores biconical.

Type: *Pileocephalus chinensis* Schn.

Genus 22. Stylocystis Léger 1899:526. Epimerite a sharply recurved cone. Spores biconical.

Type: *Stylocystis praecox* Léger.

Genus 23. Discorhynchus Labbé 1899:20. Epimerite a large globular papilla with a thin collar at the base, neck short. Spores biconical, slightly curved.

Type: *Discorhynchus truncatus* (Léger) Labbé.

Genus 24. Steinina Léger and Duboscq 1904:352. Epimerite a short mobile digitiform process changing into a flattened disc. Spores biconical.

Type: *Steinina ovalis* (Stein) L & D.

Genus 25. Anthorhynchus Labbé 1899:19. Epimerite a large fluted flattened disc. Spores biconical, extruded in chains laterally.

Type: *Anthorhynchus sophiae* (Schn.) Labbé.

Genus 26. Sciadophora Labbé 1899:18. Epimerite a large sessile disc with crenulate periphery. Protomerite with numerous backwardly-directed vertical laminations. Spores biconical.

Type: *Sciadophora phalangii* (Léger) Labbé.

Genus 27. Amphorocephalus Ellis 1913:462. Epimerite a sessile peripherally fluted disc set upon a short dilated neck. Protomerite constricted superficially across middle. (Spores unknown.)

Type: *Amphorocephalus amphorellus* Ellis.

Genus 28. Pyxinia Hammerschmidt 1838:357. Epimerite a flat crenulate crateriform disc from the center of which rises a long or short style. Spores biconical.

Type: *Pyxinia rubecula* Hamm.

Genus 29. Schneideria Léger 1892:153. Epimerite sessile, a thick horizontal disc with milled border, from center of which projects up a short style. No protomerite in adults. Spores biconical.

Type: *Schneideria mucronata* Léger.

Genus 30. *Asterophora* Léger 1892:129. Epimerite like *Schneideria*, with longer style. Spores cylindro-biconical.

Type: *Asterophora mucronata* Léger.

Genus 31. *Beloides* Labbé 1899:27. Epimerite a short stout neck with spiny globule at apex. Spores biconical.

Type: *Beloides firmus* (Léger) Labbé.

Genus 32. *Actinocephalus* Stein 1848:196. Epimerite sessile or with short neck, at apex of which are eight to ten short sharp or simple digitiform processes. Spores biconical.

Type: *Actinocephalus conicus* (Duf.) Frantz.

Genus 33. *Taeniocystis* Léger 1906:307. Epimerite small sessile sphere set with six or eight recurved hooks. Deutomerite divided by septa into many linear segments. Spores biconical.

Type: *Taeniocystis mira* Léger.

Genus 34. *Stictospora* Léger 1893:129. Epimerite with a short neck, a spherical crateriform ball with twelve backwardly-directed laminations set close to neck. Spores biconical, slightly curved.

Type: *Stictospora provincialis* Léger.

Genus 35. *Bothriopsis* Schneider 1875:596. Epimerite sessile, small, ovoidal, set with six or more long slender filaments directed upward. Spores biconical. Protomerite wider than deutomerite, septum convex upward.

Type: *Bothriopsis histrio* Schn.

Genus 36. *Coleorhynchus* Labbé 1899:23. Protomerite a shallow disc with scalloped cape down over upper part of deutomerite. Spores biconical.

Type: *Coleorhynchus heros* (Schn.) Labbé.

Genus 37. *Legeria* Labbé 1899:24. Protomerite broader than deutomerite, septum convex upward, spores cylindro-biconical. (Epimerite unknown.)

Type: *Legeria agilis* (Schn.) Labbé.

Genus 38. *Geneiorhynchus* Schneider 1875:594. Epimerite a tuft of short bristles at apex of a long slender neck, spores cylindro-biconical.

Type: *Geneiorhynchus monnieri* Schn.

Genus 39. *Hoplorhynchus* Carus 1863:570. Epimerite a flat disc with eight to ten short digitiform processes at apex of a long neck. Spores biconical.

Type: *Hoplorhynchus oligacanthus* (von Sieb.) Schn.

Genus 40. *Phialoides* Labbé 1899:24. Epimerite a cushion set peripherally with stout teeth around the base a collar larger than the cushion, upon a long slender neck. Spores biconical.

Type: *Phialoides ornata* (Léger) Labbé.

Family 8. *Acanthosporidae* Léger 1892:167. Sporonts solitary, epimerites complex. Cyst dehiscence by simple rupture. Spores with equatorial and polar spines.

Genus 41. *Acanthospora* Léger 1892:145. Epimerite a simple conical knob. Spores biconical with a row of equatorial and one of polar spines.

Type: *Acanthospora pileata* Léger.

Genus 42. *Corycella* Léger 1892:144. Epimerite globular, with eight large recurved hooks. Spores biconical with one row of polar spines.

Type: *Corycella armata* Léger.

Genus 43. *Prismatospora* Ellis 1914:215. Epimerite subglobular with eight lateral recurved hooks. One row of spines at each pole. Spores hexagonal.

Type: *Prismatospora evansi* Ellis.

Genus 44. *Ancyrophora* Léger 1892:146. Epimerite globular with five to ten backwardly-directed digitiform processes. Spores biconical with one row of equatorial and one of polar spines.

Type: *Ancyrophora gracilis* Léger.

Genus 45. *Cometoides* Labbé 1899:29. Epimerite a globe with six to eight long slender filaments directed upward. Spores cylindro-biconical with one row of polar and two of equatorial spines.

Type: *Cometoides crinitus* (Léger) Labbé.

Family 9. *Menosporidae* Léger 1892:168. Sporonts solitary. Epimerite a large cup bordered with hooks and placed on a long slender neck. Cyst dehiscence by simple rupture. Spores crescentic, smooth.

Genus 46. *Menospora* Léger 1892:151, 168. Characters of the family.

Type: *Menospora polyacantha* Léger.

Family 10. *Stylocephalidae* Ellis 1912:25. Sporonts solitary, epimerites varied. Nucleus ovoidal. Dehiscence by pseudocyst. Spores hat-shaped, in chains.

Genus 47. *Stylocephalus* Ellis 1912:25. Dilated papilla at end of a long neck. Spores hat-shaped. Cysts covered with minute papillae.

Type: *Stylocephalus oblongatus* (Hamm.) Wats.

Genus 48. *Bulbocephalus* Watson 1916b:66. Epimerite a dilated papilla in middle of a long slender neck.

Type: *Bulbocephalus wardi* Wats.

Genus 49. *Sphaerorhynchus* Labbé 1899:32. Epimerite a small sphere at the end of a long slender neck.

Type: *Sphaerocystis ophioides* (Schn.) Labbé.

Genus 50. *Cystocephalus* Schneider 1886:99. Epimerite a large lance-shaped papilla at end of a short neck. Spores hat-shaped.

Type: *Cystocephalus algerianus* Schn.

Genus 51. *Oocephalus* Schneider 1886:101. Epimerite a sphere at apex of a short stout neck.

Type: *Oocephalus hispanus* Schn.

Genus 52. *Lophocephalus* Labbé 1899:31. Sessile crateriform disc with crenulate periphery, set at the base with many short upwardly-directed digits.

Type: *Lophocephalus insignis* (Schn.) Labbé.



Family 11. Dactylophoridae Léger 1892:165. Sporonts solitary, epimerites highly complex, asymmetric, digitate. Cyst dehiscence by pseudocyst, spores elongate-cylindrical. Parasites in Chilopods.

Genus 53. *Echinomera* Labbé 1899:16. Epimerite an eccentric cone with eight or more short upwardly-directed digitiform processes, persistent. Cyst dehiscence by simple rupture, spores cylindrical, extruded in chains.

Type: *Echinomera hispida* (Schn.) Labbé.

Genus 54. *Rhopalonia* Léger 1893:1285. Epimerite a subspherical cushion with ten or more short thick outwardly directed digits. Pseudocyst. Spores cylindrical.

Type: *Rhopalonia geophili* Léger.

Genus 55. *Trichorhynchus* Schneider 1882:438. Protomerite with long slender neck dilated at end in an eccentric cone. Cyst-dehiscence by pseudocyst, spores cylindrical to ellipsoidal.

Type: *Trichorhynchus pulcher* Schn.

Genus 56. *Seticephalus* Kamm 1922. Epimerite a dense tuft of short upwardly-directed brush-like bristles on top of the broad flat protomerite.

Type: *Seticephalus elegans* (Pinto) Kamm.

Genus 57. *Dactylophorus* Balbiani 1889:41. Protomerite dilated laterally at the top and set with peripheral digitiform processes. Cyst dehiscence by pseudocyst, spores cylindrical.

Type: *Dactylophorus robustus* Leger.

Genus 58. *Nina* Grebnecki 1873: ? Protomerite two long lobes fused at one end, set peripherally with teeth and long filaments. Cyst dehiscence by pseudocyst. Spores long-ovoidal, in chains obliquely.

Type: *Nina gracilis* Grebnecki.

Genus 59. *Acutispora* Crawley 1903:632. Epimerite not described. Spores long, ellipsoidal with a lengthwise-directed rod at each end. Cyst dehiscence by pseudocyst.

Type: *Acutispora macrocephala* Crawl.

#### GENERA OF UNCERTAIN POSITION

Genus 60. *Metamera* Duke 1910:261. Epimerite an eccentric cone set peripherally with numerous branched digitiform processes. Cyst dehiscence by simple rupture. Spores obese biconical.

Type: *Metamera schubergi* Duke.

Genus 61. *Agrippina* Strickland 1912:108. Sporonts solitary, epimerite a circular disc armed with peripheral digitiform processes, on a short neck. Spores long ovoidal.

Type: *Agrippina bona* Strick.

Genus 62. *Ganymedes* Huxley 1910:155. Sporonts associative. A motile stalked sphere at anterior end, cup at posterior end. No septum, no true epimerite. Cysts spherical. Alimentary tract of Crustacea.

Type: *Ganymedes anaspidis* Hux.

Genus 63. *Nematoides* Mingazzini 1891:233. Dicystid, no septum in sporonts. Epimerite forked, at apex of a long neck.

Type: *Nematoides fusiformis* Ming.

## A GROUP OF TABLES SHOWING THE PHYLOGENETIC RELATIONSHIPS OF GREGARINES

*Table 1. Showing the Intermediate Position of Two Families, LECUDINIDAE AND POLYRHABDINIDAE*

	Septum	Epimerite, character	Spores	Host	Habitat
Tribe Acephalina	Absent	Absent	Biconical or with dissimilar poles	Echinoderms, marine and terrestrial Annelids, a few Arthropods	Generally coelomic
Family Lecudinidae	Absent	Present, simple	Dissimilar poles	Marine Annelida	Digestive tract
Family Polyrrhabdinidae	Present	Present, varied	?	Marine Annelida	Digestive tract
Tribe Cephalina	Present	Present, varied	All poles alike	Arthropoda	Digestive tract

*Table 2. Showing Relationships of the Families of the Tribe Cephalina*

Family	Sporont	Epimerite	Development	Cyst dehiscence	Spores	Host	Remarks
1. Lecudinidae 2. Polyrrhabdinidae 3. Cephaloidophoridae	Twos	Absent	Intracellular	Simple rupture	Ovoidal with equatorial line	Crustacea	No septum in satellites
4. Stenophoridae	Solitary	Absent or rudimentary	Intracellular	Simple rupture	Ovoidal with equatorial line	Diplopods	
5. Gregarinidae	Solitary or in associations up to 12	Simple, symmetrical	Extra-cellular	Spore-ducts or simple rupture	Ellipsoidal	Insects chiefly	
6. Didymophyidae	Associations of 2 or 3	Small, simple papilla	"	Simple rupture	Ellipsoidal	Crustacea and Coleoptera	
7. Actinocephalidae	Solitary	Complex	"	Simple rupture	Irregular or biconical or cylindrical-biconical	Insects and Chilopods	
8. Acanthosporidae	Solitary	Complex	"	Simple rupture	With equatorial and polar spines	Insects	
9. Menosporidae	Solitary	Long neck, cup with spines at top	"	Simple rupture	Crescentic	Insects	
10. Stylocephalidae	Solitary	Long neck (except one genus) with simple apex	"	Pseudocyst	Irregular brown or black	Insects	
11. Dactylophoridae	Solitary	Highly complex asymmetric digitate	"	Pseudocyst	Elongate-cylindrical	Chilopods	

Table 3. Showing Relationships Between Genera in the Family Gregarinidae

Genus	Sporont	Epimerite	Cyst dehiscence	Spores	Remarks
1. Leidyana	Solitary	Sessile globe	Spore-ducts	Barrel-shaped, in chains	
2. Gregarina	In twos	Simple globular or cylindrical papilla	Spore-ducts	Barrel-shaped, in chains	
3. Protomagalbaensia	Several	?	?	Barrel-shaped, with spine at each corner	Sporonts attenuate, attachment often lateral
4. Gamocystis	In twos	?	Spore-ducts, sporulation partial	Cylindrical	Protomerite only in trophic stages
5. Hyalospora	In twos	Simple globular knob	Simple rupture	Ellipsoidal	Endoplasm yellow-orange
6. Hirmocystis	Two to 12	Small cylindrical papilla	Simple rupture	Ovoidal	
7. Euspora	In twos	?	Simple rupture	Prismatic	
8. Sphaerocystis	Solitary	?	Simple rupture	Ovoidal	Protomerite only in trophic stages
9. Cnemidospora	Solitary	?	Simple rupture	Ellipsoidal	Protomerite one-half gray, other yellow-green
10. Uradiophora	In twos	Elongate papilla	Simple rupture	Spherical or subspherical, in chains	Deutomerite with small appendix, Crustacea
11. Pyxinoides	In twos	Slightly stalked globular papilla with 16 longitudinal furrows and a small cone at apex		?	Crustacea

Table 4. Showing Relationships Between Genera in the Family Actinocephalidae

Genus	Epimerite	Spores	Remarks
1. Amphoroides	Sessile globular papilla	Curved biconical	
2. Pileocephalus	Short dilated neck, lance-shaped cone at apex	Biconical	
3. Stylocystis	Recurved sharply pointed cone	Biconical	
4. Discorhynchus	Short neck, large globe with thin collar around base	Biconical, slightly curved	
5. Steinina	A short mobile digitiform process changing into a flat crenulate disc	Biconical	
6. Anthorhynchus	Sessile large fluted flattened disc	Biconical	Extruded in chains, laterally
7. Sciadophora	A large sessile peripherally crenulate disc	Biconical	Protomerite with numerous backwardly-directed vertical laminations
8. Amphorocephalus	Concave peripherally crenulate fluted disc set upon a short dilated neck	?	



Table 4. (Continued)

Genus	Epimerite	Spores	Remarks
9. Pyxinia	Flat crenulate crateriform disc from center of which rises a long or short style	Biconical	
10. Schneideria	Sessile, a thick horizontal disc with milled border, short style projecting up from center	Biconical	No protomerite in adults; a degenerate rather than rudimentary character
11. Asterophora	Like last, with central style longer	Cylindro-biconical	
12. Beloides	Short stout neck with spiny globe at apex	Biconical	
13. Actinocephalus	Sessile or with short neck, at apex 8 to 10 short sharp spines or simple processes	Biconical	
14. Taeniocystis	Small sessile sphere set with 6 or 8 recurved hooks	Biconical	Deutomerite divided by septa into many linear segments
15. Stictospora	Short neck, spherical crateriform ball with 12 backwardly-directed laminate filaments set close to neck	Biconical, slightly curved	
16. Bothriopsis	Sessile, very small, ovoidal, with 6 or more long slender filaments directed upward	Biconical	Protomerite wider than deutomerite, septum convex upward
17. Coleorhynchus	?	Biconical	Septum convex upward. Prot. a shallow disc with scalloped cape over deutomerite
18. Legeria	?	Cylindro-biconical	Protomerite broader than deutomerite, septum convex upward
19. Geneiorhynchus	Long slender neck, tuft of short bristles at apex	Cylindro-biconical	
20. Hoplorhynchus	Long neck, flat disc with 8 to 10 digitiform processes at apex	Biconical	
21. Phialoides	Long slender neck, at apex a broad cushion with peripheral teeth surrounded at base with a collar larger than the cushion	Biconical	

The epimerites of this family are surprisingly well correlated. The genera with short necks form a regular succession; the simple globe (1) becomes slightly modified (2), (3); then a disc develops at the base (4), (5), (6), (7), (8); with a style rising in the center (9), (10). This seems to be the end of one line of development.

The simple sessile or nearly sessile globule becomes spiny (12), (13); the spines become simple digitiform processes or recurved hooks (14); the recurved hooks become attached to the neck along their whole length (15). The processes change into long slender filaments (16)—and probably (17) and (18). The neck becomes long and slender, and at the apex there develops a tuft of short bristles (19), a flat disc with 8 to 10 peripheral digits (20), or stout teeth (21).

Table 5. Showing the Relationships Between the Genera in the Family Acanthosporidae

Genus	Epimerite	Spores
1. Acanthospora	Simple conical knob	Biconical, row of equatorial and one of polar spines
2. Corycella	Globular, with 8 large recurved hooks	Biconical, one row of polar spines
3. Prismatospora	Subglobular, with 8 lateral recurved hooks	One row of spines at each pole. Hexagonal
4. Ancyrophora	Globular, with 5 to 10 backwardly directed digitiform processes	Biconical, with one row of equatorial and one of polar spines.
5. Cometoides	Globe, with 6 to 8 long slender filaments directed upward	Cylindro-biconical, with one row of polar and two of equatorial spines

Table 6. Showing Relationships Between the Genera in the Family Stylocephalidae

Genus	Epimerite	Spores	Remarks
1. Stylocephalus	Long neck, dilated papilla at apex	Hat-shaped	Cysts covered with small papillae
2. Bulbocephalus	Long neck, dilated papilla midway	?	
3. Sphaerorhynchus	Long neck, small sphere at apex	?	
4. Cystocephalus	Short stout neck, large lance-shaped papilla at apex	Hat-shaped	
5. Oocephalus	Short neck with sphere at apex	?	
6. Lophocephalus	Sessile crateriform disc with crenulate periphery, set at base with many short upwardly-directed digits	Hat-shaped	

I can see very little relationship between the genera of this family as a whole. (1), (2), and (3) are related, as are (4) and (5), but the three groups seem to bear no epimeritic relationship whatever. The hat-shaped spores, however, connect the seemingly aberrant genus (6), with the type.

Table 7. Showing Relationships Between the Genera in the Family Dactylophoridae

Genus	Character of protomerite or epimerite	Cyst dehiscence	Spores	Remarks
1. Echinomera	Epimerite an eccentric cone with eight or more short upwardly-directed digitiform processes, persistent	Simple rupture	Cylindrical in chains	
2. Rhopalonia	Epimerite a subspherical cushion with ten or more short thick outwardly-directed digits	Pseudocyst	Cylindrical	No protomerite in adult
3. Trichorhynchus	Protomerite with long slender neck dilated at end in an eccentric cone	Pseudocyst	Cylindrical to ellipsoidal	
4. Seticephalus	A dense tuft of short upwardly-directed brush-like bristles on top of a broad flat protomerite	?	?	
5. Dactylophorus	Protomerite dilated laterally with peripheral digitiform processes	Pseudocyst	Cylindrical	
6. Nina	Protomerite two long lobes fused at one end, set peripherally with teeth and long filaments	?	Long-ovoidal	Spores in chains obliquely
7. Acutispora	?	Pseudocyst	Long-ellipsoidal with a lengthwise-directed rod at each end	



# SYNOPSSES OF THE GREGARINES FROM VARIOUS GROUPS OF THE ANIMAL KINGDOM

## LIST OF SPECIES FOUND IN THE PHYLUM COELHELMINTHES\*

PARASITE	Host
<b>LECUDINIDAE</b>	
<i>Lecudina pellucida</i> (Köl liker) Mingazzini	<i>Nereis cultrifera</i>
Type species	<i>N. beaucourdrayi</i> Aud.
<i>Lecudina leuckarti</i> Mingazzini	<i>Sagitta</i> sp.
<i>Lecudina aphroditae</i> (Lankester) Kamm	<i>Aphrodite aculeata</i>
<i>Lecudina elongata</i> (Mingazzini) Kamm	<i>Lumbriconereis impatiens</i> Clap.
<i>Lecudina heterocephala</i> (Mingazzini) Kamm	<i>Nephthys scolopendroides</i> delle Chiaje
<i>Lecudina polydorae</i> (Léger) Kamm	<i>Polydora agassizi</i> Clap.
	<i>P. ciliata</i>
<i>Lecudina</i> sp. Saint-Joseph	<i>Polymnia nebulosa</i> M.
	<i>Notomastus exsertilis</i> N. S.
<i>Lecudina legeri</i> (Brasil) Kamm	<i>Petaloproctus terricola</i> Qfg.
<i>Lecudina</i> sp. Faria, Cunha, and Fonseca	<i>Glycera convoluta</i> Kef.
	<i>Polydora socialis</i> Schm.
<b>POLYRHABDINIDAE</b>	
<i>Polyrhabdina spionis</i> (Köl liker) Mingazzini	<i>Scololepsis fuliginosa</i>
Type species	<i>S. ciliata</i>
<i>Polyrhabdina brasili</i> Caullery and Mesnil	<i>Spio martinensis</i>
<i>Polyrhabdina pygospionis</i> Caullery and Mesnil	<i>Pygospionis seticornis</i>
<i>Sycia inopinata</i> Léger	<i>Audouinia Lamarckii</i>
Type species	
<i>Ulivina elliptica</i> Mingazzini	<i>Audouinia filigera</i> (d. Chiaje)
Type species	<i>A. tentaculata</i> Mont.
	<i>Petaloproctus terricola</i> Qfg.
	<i>Nicolea venustula</i> Mont.
	<i>Polymnia nebulosa</i> Mont.
<i>Ulivina rhynchoboli</i> (Crawley) Kamm	<i>Rhynchobolus americanus</i> Ver.
<b>GENUS OF UNCERTAIN POSITION</b>	
<i>Metamera schubergi</i> Duke	<i>Glossosiphonia complanata</i>
Type species	<i>Hemiclepsis marginata</i>
<i>Metamera</i> sp. Ellis	<i>Clepsine elongata</i>
<b>SPECIES OF UNCERTAIN POSITION</b>	
? <i>Taeniocystis légeri</i> Cognetti de Martiis	<i>Kynotus Pillarelli</i>

## Family LECUDINIDAE Kamm (nov. fam.)

Epimerite symmetrical, simple. Body non-septate. Spores ovoidal, asymmetrical, thickened at one pole. Intestine of marine annelids.

\*The parasites are arranged in chronological order under each genus in this and all similar succeeding lists.

## DISCUSSION OF THE NEW FAMILY LECUDINIDAE

The type genus of this family, *Lecudina* was named by Mingazzini in 1891. Two years later Léger, working independently, designated a new genus *Doliocystis* for the species described by Mingazzini. The earlier work has been overlooked by subsequent workers while the name used by Léger has come into frequent usage, the genus being raised to family rank (*Doliocystidae*) by Labbé, in 1899.

In Table I of Chapter II, is shown the intermediate position of the family *Lecudinidae* and the somewhat related family, the *Polyrhadinidae*. The *Lecudinidae* are related to the Tribe *Acephalina*, for they are non-septate, there being but one division in the body at all stages of development.

All the members of the Tribe *Cephalina*, on the other hand, are characterized by the presence of a septum, which divides the body into a protomerite and deutomerite, if not in the adult, at least in the trophic stages of development. When the septum is absent from the adult, it is clearly a degenerative rather than a rudimentary character, all other generic features conforming to the type.

(Cf. *Schneideria*, *Sphaerocystis*, *Rhopalonia*, *Gamocystis*.)

The *Lecudinidae*, however, possess only the epimeritic demarkation from the rest of the body, and when this structure disappears, the body is unilocular. Léger (1893) remarks:

. . . la grégarine présente toujours deux segments: le segment intra-cellulaire ou *épimérite*, et le segment extra-cellulaire dans lequel s'est porté le noyau. C'est donc seulement à ce moment que la grégarine se montre comme une véritable dicystidée. . . . les jeunes individus abandonnent leur *épimérite* et deviennent libres dans l'intestin, présentant a lors toutes les apparences de véritable Monocystis . . . .

In the type species, *Lecudina pellucida* (Köll.) Ming., there is a differentiation in the protoplasm of the anterior end (what would be the protomerite in polycystids) from that of the remainder of the body. This was illustrated by Kölliker (my fig. 126) but not mentioned by Léger in 1893. Brasil (1909) illustrates this differentiation clearly in both trophozoite and sporont (my figs. 134 and 135).

If normally present, and I have no doubt that it is but often not mentioned or discovered, this character is an important one in assigning the family in question to an intermediate position between the monocystids and the polycystids.

In its cyst-formation and spore type, the family follows the polycystid type.

After the above had been written, this statement from Minchin (1903) was found:

The possession of an epimerite is a feature used for classifying which the Gregarines, and the legion Eugregarinae is separated into the two sub-orders Cephalina and Acephalina, according to the presence or absence of this appendage. As a general rule the forms which

possess an epimerite have the body behind it divided into protomerite and deutomerite by a septum, and have hence been termed Polycystida . . . , while those without an epimerite are also without a septum; hence Monocystida . . . But in one family, Doliocystidae, Labbé, an epimerite is present, and may attain a considerable size . . . without any septum dividing the rest of the body . . . It is purely a matter of definition whether those forms be considered as Cephalina without a septum, or as Monocystis with an epimerite. The Cephalina in which the body is non-septate are sometimes distinguished as Dicystida from those in which there is a distinct protomerite and deutomerite (Tricystida). These terms are to be understood, however, in a purely descriptive sense, and cannot be used for classificatory purposes, as there is no doubt that many dicystid species are derived from tricystid forms secondarily, by obliteration of the protomerite . . . . On the other hand, such forms as the Doliocystidae . . . . appear to be truly and primitively dicystid, and are to be regarded as intermediate forms transitional from Acephalina to Cephalina.

#### Genus LECUDINA MINGAZZINI 1891: 469

Body non-septate, epimerite regularly simple. Spores ovoidal, thickened at one pole.

#### LECUDINA PELLUCIDA (Kölliker) Mingazzini Type species

[Figure 126]

1848	<i>Gregarina pellucida</i>	Kölliker	1848: 35
1851	<i>Gregarina pellucida</i>	Diesing	1851: 17
1859	<i>Gregarina pellucida</i>	Diesing	1859: 739
1872	<i>Monocystis nereidis</i>	Lankester	1872: 343
1891	<i>Lecudina pellucida</i>	Mingazzini	1891: 469
1893	<i>Lecudina pellucida</i>	Mingazzini	1893: 51
1893	<i>Doliocystis pellucida</i>	Léger	1893: 204
1899	<i>Doliocystis pellucida</i>	Labbé	1899: 33
1903	<i>Doliocystis pellucida</i>	Minchin	1903: 202, 327
1909	<i>Doliocystis pellucida</i>	Brasil	1909: 119
1913	<i>Doliocystis pellucida</i>	Ellis	1913: 287

Sporonts solitary, ellipsoidal or "bottle-shaped," rectangular or rounded at anterior end and broadly rounded at posterior. Nucleus spherical. Epimerite a simple small papilla.

Cysts small, dehiscence by simple rupture, spores ovoidal, 7 by 5 $\mu$ , with thickening at one pole.

Taken at Trieste, Naples, and in the Gulf of Marseilles.

Intestine of *Nereis cultrifera* Grube and *N. beaucourdrayi* Aud. Kölliker's figure indicates a differentiation in the protoplasm of the anterior end of the body from that of the remainder.

Mingazzini describes the body as nearly transparent, especially at the anterior end, and both mentions and illustrates the retractility of the anterior end within the body.



## LECUDINA LEUCKARTI Mingazzini

1860	No name	Leuckart	1860: 263
1891	<i>Lecudina Leuckarti</i>	Mingazzini	1891: 469
1893	<i>Lecudina Leuckarti</i>	Mingazzini	1893: 51

Similar to the type species, the anterior end not constricted bottle-like.  
Intestine of *Sagitta* sp.

## LECUDINA APHRODITAE (Lankester) Kamm

[Figure 125]

1863	<i>Monocystis aphroditae</i>	Lankester	1863: 90, 94
1871	Unnamed	Stuart	1871: 498
1899	<i>Doliocystis aphroditae</i>	Labbé	1899: 33
1903	<i>Doliocystis aphroditae</i>	Minchin	1903: 176, 202, 326
1909	<i>Doliocystis aphroditae</i>	Brasil	1909: 120
1922	<i>Lecudina aphroditae</i>	Kamm	1922 (this paper)

One-half inch in length. "This is the only unilocular form of *Gregarina* which at present has been found provided with a proboscis." Lankester.

Intestine of *Aphrodite aculeata*.

## LECUDINA ELONGATA (Mingazzini) Kamm

[Figures 134 and 135]

1891	<i>Ophiodina elongata</i>	Mingazzini	1891: 471
1893	<i>Ophiodina elongata</i>	Mingazzini	1893: 53
1899	<i>Doliocystis elongata</i>	Labbé	1899: 33
1903	<i>Doliocystis elongata</i>	Minchin	1903: 327
1908	<i>Doliocystis elongata</i>	Brasil	1908: 355
1908	<i>Doliocystis elongata</i>	Brasil	1908a: 425
1909	<i>Doliocystis elongata</i>	Brasil	1909: 112
1922	<i>Lecudina elongata</i>	Kamm	1922 (this paper)

Sporonts solitary, elongate-cylindrical, attaining 500 $\mu$  by 40 $\mu$ . Protoplasm of anterior end highly specialized from that of remainder. Nucleus large, spherical, with several karyosomes.

An intracellular stage was encountered by Brasil, who thinks it may be schizogonic in character. It is possible, however, that it may have been a portion of the life-history of another parasite.

Mingazzini describes the epimerite as a "piccolo bottone sferico"; Brasil finds a long thread-like filament which penetrates to the base of the cell, which is certainly atypical.

Intestine of *Lumbriconercis impatiens* Claparede.

Taken at Naples.

In three of Mingazzini's twelve illustrations of the species, there is some indication of a septum present, the protoplasm being quite different in the two portions.

I can see no differentiation between the two genera described by Mingazzini, *Lecudina* and *Ophioidina*, from the meagre data known concerning each. The intracellular development and the spores may reveal differences, however. From the existing data, I have united the two under the name of the first-named genus, *Lecudina*.

#### LECUDINA HETEROCEPHALA (Mingazzini) Kamm

1891	<i>Ophioidina heterocephala</i>	Mingazzini	1891: 473
1893	<i>Ophioidina heterocephala</i>	Mingazzini	1893: 54
1899	<i>Doliocystis heterocephala</i>	Labbé	1899: 34
1903	<i>Doliocystis heterocephala</i>	Minchin	1903: 327
1922	<i>Lecudina heterocephala</i>	Kamm	1922 (this paper)

Sporonts very elongate, vermiform. Epimerite "a sort of papilla" at anterior end. Protoplasm of anterior end differentiated from that of body proper.

Nucleus spherical, with one or two karyosomes.

Intestine of *Nephtys scolopendroides* delle Chiaje.

#### LECUDINA POLYDORAE (Léger) Kamm

1893	<i>Doliocystis polydorae</i>	Léger	1893: 205
1899	<i>Doliocystis polydorae</i>	Labbé	1899: 33
1903	<i>Doliocystis polydorae</i>	Minchin	1903: 327
1909	<i>Doliocystis polydorae</i>	Brasil	1909: 119
1914	<i>Polyrhabdina polydorae</i>	Caullery and Mesnil	1914: 520
1922	<i>Lecudina polydorae</i>	Kamm	1922 (this paper)

Epimerite similar to that described for the type species, but larger. "Epimerite a la forme d'un tronc de cone a petite base inferieure et il se continue directement avec l'extremite anterieure du second segment, allongee en forme de col." Léger.

Intestine of *Polydora agassizi* Clap.; *P. ciliata*.

Taken in the Gulf of Marseilles, France.

#### LECUDINA sp. Saint-Joseph

1907	<i>Doliocystis</i> sp.	Saint-Joseph	1907: 145, 172, 173
1911	<i>Doliocystis</i> sp.	Sokolow	1911: 287
1922	<i>Lecudina</i> sp.	Kamm	1922 (this paper)

Measurements are given of sporonts from various polychaetes, as follows:  $84\mu$  by  $29\mu$ ;  $470\mu$  by  $63\mu$ ;  $300\mu$  by  $48\mu$ . It is quite possible that several species are involved, but no description is given of any one.

Intestine of *Polymnia nebulosa* M.; *Notomastus exsertilis* N.S.; and *Petaloproctus terricola* Qfg.

#### LECUDINA LEGERI (Brasil) Kamm

1909	<i>Doliocystis legeri</i>	Brasil	1909: 71, 123
1911	<i>Doliocystis legeri</i>	Sokolow	1911: 284
1922	<i>Lecudina legeri</i>	Kamm	1922 (this paper)

Sporonts cylindrical,  $100\mu$  by  $25\mu$ . Nucleus ovoidal, with one karyosome. Epimerite a rhizoid filament which penetrates to the base of the host-cell (Brasil).

Cysts small,  $45\mu$  in diameter, spores typical, releasing eight sporozoites.

Intestine of *Glycera convoluta* Kef.

Taken on the Mediterranean Coast.

#### LECUDINA sp. Faria, Cunha, and Fonseca

1918	<i>Doliocystis</i> sp.	Faria, Cunha, and Fonseca	1918: 17
1922	<i>Lecudina</i> sp.	Kamm	1922 (this paper)

Sporonts spindle-shaped, nucleus spherical.

Host: *Polydora socialis* Schmerda.

Taken near Rio de Janeiro, Brazil.

Not enough data exists to definitely fix the position of this species.

#### Family POLYRHABDINIDAE Kamm 1922 (this paper)

Polycystid (septate) gregarines inhabiting the digestive tract of polychaetes. Epimerites varied.

#### DISCUSSION OF THE NEW FAMILY POLYRHABDINIDAE

The true septate intestinal gregarines of marine annelids fall under three genera, which are placed in various positions by different workers on the subject:

(a) Two genera were described very meagerly by Mingazzini in 1891 under one name, Polyrrhabdina, two very different parasites being found in the same host material. The one has been removed to the Schizogregarines (Selenidium), while the other represents the genus as named, and is a pyriform septate species which possesses an epimerite in the shape of a corona of hooks.<sup>1</sup>

(b) The genus *Sycia* Léger 1892 is characterized by its septate sporonts and unique epimerite in the form of a large rounded papilla with a thick

<sup>1</sup> Mingazzini's description follows: . . . specie dimorfe. Individue a forme di nematode e piriformi. I primi hanno il corpo allungato fusiforme e la cuticula striata longitudinalmente da rialzi numerosi finissimi.



ring or collar around the base. The deutomerite of the adult sporont, only, contains numerous elongate crescentic or ellipsoidal inclusions probably "reserve protoplasm."

(c) The third genus, *Ulivina* Mingazzini 1891, has little to characterize it. In fact so little is known concerning its development that it cannot be placed with either of the two named genera and hence must stand distinct until its position shall have been proven. The epimerite, is simple so far as known and cyst and spores are unknown.

The cysts and spores are still unknown for all three genera.

Since a septum is present without exception in all three, they must be included in the suborder Cephalina, but stand near the borderline with the Acephalina because of their presence only in polychaetes.

#### Genus POLYRHABDINA Mingazzini 1891:229

(*Polyrhabdina* Labbé 1899:48)

Septate, sporonts flattened, ovoidal, epimerite a corona of hooks. Intestine of polychaetes of the family Spionidae. (Cyst and spores unknown.)

#### POLYRHABDINA SPIONIS (Kölliker) Mingazzini Type Species

[Figures 128, 129]

1848	<i>Gregarina Spionis</i>	Kölliker	1848: 4
1851	<i>Gregarina Spionis</i>	Diesing	1851: 18
1891	<i>Polyrhabdina Spionis</i>	Mingazzini	1891: 229
1893	<i>Polyrhabdina Spionis</i>	Mingazzini	1893: 56
1903	<i>Doliocystis</i> sp.	Minchin	1903: 327
1914	<i>Polyrhabdina spionis</i>	Caullery and Mesnil	1914: 516

Septum present. Sporonts 100 by 35 $\mu$ , ellipsoidal, nucleus spherical, one large karyosome.

Epimerite a flattened apical corona of 8 to 10 ameoboid digitiform processes frequently bifurcate.

Development extracellular. Cyst and spores unknown.

Intestine of *Scololepsis fuliginosa*; *S. ciliata* (?).

Taken at Naples.

Minchin mentions a species from the same host, but places it in the genus *Doliocystis*. Since no data is given and the hosts are identical, it is placed here.

#### POLYRHABDINA BRASILI Caullery and Mesnil

1914	<i>Polyrhabdina brasili</i>	Caullery and Mesnil	1914: 518
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Sporonts ovoidal, 200 $\mu$  in length. Epimerite characteristic, but spines shorter than type.

Cyst and spores unknown.

Host: *Spio martinensis*.

## POLYRHABDINA PYGOSPIONIS Caullery and Mesnil

1914 *Polyrhabdina pygospionis* Caullery and Mesnil 1914: 520

No description given.

Host: *Pygospionis seticornis*.

## Genus SYCIA Léger 1892: 52

Polycystid intestinal parasite of marine annelids. Epimerite knobbed, bordered by a thick ring. Protomerite subspherical, deutomerite conical, with numerous inclosures.

## SYCIA INOPINATA Léger Type Species

[Figures 118 and 119]

1892	<i>Sycia inopinata</i>	Léger	1892: 52, 90
1899	<i>Sycia inopinata</i>	Labbé	1899: 34
1903	<i>Sycia inopinata</i>	Minchin	1903: 203, 326
1909	<i>Sycia inopinata</i>	Brasil	1909: 121

Septate gregarine, ellipsoidal. No dimensions given. Ratio LP : TL :: 1:6; WP : WD :: 1:1.5. Protomerite conoidal, broadest at septum. Deutomerite ellipsoidal, tapering rapidly to a sharp point. Nucleus large, spherical, one karyosome.

Epimerite an elongate papilla upon a short neck around which is a collar a little larger than the papilla itself.

Intestine of *Audouinia Lamarkii* (*A. tentaculata*—Brasil).

Taken at Belle-Isle-sur-Mer, France.

Caullery and Mesnil (1914) give the host name as the latter above, and note

. . . c'est une espèce voisine, sinon identique, que Mingazzini (1891) a dénommée *Ulivina* n. g. *elliptica*

but since the cyst and spores of both species are unknown, this cannot at present be determined.

This species possesses characteristic elongate crescentic or biconical inclusions in the deutomerite only of adult sporonts. (Fig. 119). Léger offers the hypothesis that they may be condensations of protoplasm in reserve masses.

Brasil found this species with its epimerite and the inclusions, thus verifying Léger's work of sixteen years previous.

## Genus ULIVINA Mingazzini 1891: 235

Body elongate-ellipsoidal, "external membrane continuous around animal." Protomerite the more dense. Epimerite simple, spores unknown. Intestine of marine polychaetes.

## ULIVINA ELLIPTICA Mingazzini Type Species

[Figure 127]

1891	<i>Ulivina elliptica</i>	Mingazzini	1891: 235
1899	<i>Ulivina elliptica</i>	Labbé	1899: 34
1903	<i>Ulivina elliptica</i>	Minchin	1903: 203, 326
1907	<i>Ulivina elliptica</i>	Saint-Joseph	1907: 164, 174

Sporonts solitary, ellipsoidal, tapering to a sharply rounded posterior end. Nucleus ovoidal, two or three karyosomes. Dense and opaque. No dimensions given by the original author. Ratio LP:TL::1:4 to 7; WP:WD::1.1:1.

Saint-Joseph mentions dimensions as 150 by 90 $\mu$ ; 75 by 33 $\mu$ . He illustrates (his fig. 106) a trophozoite with a simple, small, papillate epimerite.

Taken at Naples and off the coast of France.

Intestine of *Audouinia filigera* (delle Chiaje); *A. tentaculata* Mont., *Petaloproctus terricola* Qfg., *Nicolea venustula* Mont., and *Polymnia nebulosa* Mont.

## ULIVINA RHYNCOBOLI (Crawley) Kamm

1897	Unnamed	Porter	1897a: 8
1903	<i>Doliocystis rhyncoboli</i>	Crawley	1903: 56
1913	<i>Doliocystis rhyncoboli</i>	Ellis	1913: 287
1922	<i>Ulivina rhyncoboli</i>	Kamm	1922 (this paper)

Sporonts attain 700 $\mu$  in length. A distinct septum, with protoplasm in protomerite the more dense. Epimerite a small pointed papilla with a long slender filament at the end. Nucleus small, spherical.

Intestine of *Rhynchobolus americanus* Verrill.

While the epimerite is described for this and for the preceding species, I am not ready to state that it is the type for the genus.

Porter notes a peculiar attachment of the parasite while free in a watch-glass to the glass, being attached by the anterior end of the protomerite with such force that the animal cannot be withdrawn without destroying it.

## Genus of Uncertain Position

## METAMERA Duke 1910:261

Sporonts solitary, epimerite subconical, apex eccentric with corona of numerous branched digitiform appendages. Cyst dehiscence by simple rupture. Spores biconical.



## METAMERA SCHUBERGI Duke Type Species

[Figures 131, 132, and 133]

1910	<i>Metamera schubergi</i>	Duke	1910: 261
1913	<i>Metamera schubergi</i>	Ellis	1913: 285

Sporonts 150 by 45 $\mu$ . Deutomerite with one to three septa posterior to the nucleus. Cysts spherical, spores ovoidal 9 by 7 $\mu$ .

Epimerite subconical, apex eccentric with corona of numerous branched digitiform processes.

Taken at Heidelberg and Cambridge, Eng.

Intestine of *Glossosiphonia complanata* and *Hemiclepsis marginata*.

I am not ready to assign this species to a position in the family Dactylophoridae, as placed by the author. The method of cyst-dehiscence is different from the type for that family and the spores are not elongate cylindrical. The host is so far removed from the Chilopoda (to which the named family is confined) that I feel certain the species belongs in a group as yet undescribed. When more similar species shall have been described its position can the better be determined.

## METAMERA sp. Ellis

1913	<i>Metamera</i> sp.?	Ellis	1913:285, 287
Host: <i>Clepsine elongata</i> .			

## Species of Uncertain Position

## TAENIOCYSTIS LEGERI Cognetti de Martiis

[Figure 130]

1911	<i>Taeniocystis legeri</i>	Cognetti de Martiis	1911:247
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Polycystid gregarine, solitary, protomerite and deutomerite segmented by 16 to 19 septa. 700 to 1600 $\mu$  in length.

Epimerite, cyst, and spores unknown.

Taken at Moramanga, Madagascar.

Host: *Kynotus Pittarelli* (oligochaete). Coelomic.

The "protomerite" is divided into three segments, which is unique. The parasite is coelomic rather than intestinal, as are all other polycystid gregarines. The epimerite is unknown. For these reasons it is not placed with the type for the genus. The single nucleus seems to place it with the Protozoa; otherwise it might be a haplosporidian.

## LIST OF SPECIES FOUND IN THE PHYLUM MOLLUSCA

## Species of Uncertain Position

<i>Gregarina pterotracheae</i> (Stuart) Labbé	<i>Pterotrachea</i> sp.
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## GREGARINA PTEROTRACHEAE (Stuart) Labbé

[Figure 136]

1871	<i>Zygocystis Pterotracheae</i>	Stuart	1871: 498
1891	<i>Zygocystis Pterotracheae</i>	Mingazzini	1891: 235
1899	<i>Gregarina pterotracheae</i>	Labbé	1899: 37
1903	“ “	Minchin	1903: 338

Contour of body ovoidal, typically that of the genus *Gregarina*, biassocative. Dimensions not given. Ratio LP:TL::1:4; WP:WD::1:1.5. Protomerite dome-shaped with slight constriction in middle. Deutomerite ovoidal, well-rounded posteriorly. Epicyte unusually thick. Nucleus large, spherical, one to four karyosomes.

Cyst formed of one individual seen, embedded in muscular tissue of host.

Coelom of *Pterotrachea* sp.

Taken at Odessa.

This species is regarded as of uncertain position because it is the first species of the genus *Gregarina* to be found in the body-cavity of a host. It is the only species described from the molluscs, where one would not expect to find a polycystid and biassocative gregarine. This phylum certainly offers splendid research opportunities, if not to substantiate to repudiate the above work.

Stuart describes in detail the motion of the species, and because I believe it is the first good record of the movements of gregarines, it is reproduced here, as follows:

Die Bewegungen des Thieres sind schlängelnder Art, aber neben den Hauptcontractionen, als deren Resultat die Vorwärtsschiebung der Gregarine erscheint, bemerkt man eine Reihe partieller Contractionen, welche die äusseren Contouren des Körpers wellenförmig umändern. Bei diesen Contractionen wird die weiche innere Körnermasse hin und hergeschoben und nimmt die durch die partiellen Gestaltänderungen des contractilen Schlauches gebildeten Innenräume ein. Der Nucleus folgt diesen Bewegungen in beschränktem Masse mit.

## LIST OF SPECIES FOUND IN THE CLASS CRUSTACEA OF THE PHYLUM ARTHROPODA

PARASITE	HOST
DIDYMOPHYIDAE	
<i>Didymophyes longissima</i> (von Siebold) Frantzius	<i>Gammarus pulex</i> von Sieb. <i>Orchestia littorea</i>
GREGARINIDAE	
<i>Uradiorhynchus cuenoti</i> (Mercier) Mercier	<i>Atyaephyra Desmaresti</i> Millet
Type species	
<i>Pyxinoides balani</i> (Köl liker) Trégouboff	<i>Balanus pusillus</i> Ecker <i>B. tintinnabulum</i> L. <i>B. amphitrite</i> Darw. <i>B. eburneus</i> Gould
Type species	
<i>Pyxinoides thamali</i> (Léger and Duboscq) Trégouboff	<i>Chthamalus stellatus</i> Ranz.

## CEPHALOIDOPHORIDAE

*Cephaloidophora conformis* (Diesing) Léger  
and Duboscq

*Cephaloidophora communis* Mawrodiadi  
Type species

*Cephaloidophora fossor* (Léger and Duboscq)  
Trégouboff

*Cephaloidophora ocellata* (Léger and Duboscq)  
Kamm

*Cephaloidophora maculata* Léger and Duboscq

*Cephaloidophora talitri* Mercier

*Cephaloidophora olivia* (Watson) Kamm

*Cephaloidophora nigrofusca* (Watson) Kamm

*Cephaloidophora delphinia* (Watson) Kamm

*Cephaloidophora ampelisca* (Nowlin and  
Smith) Kamm

*Pachygraspus marmoratus* Fabr.

*Balanus improvisus* Darw.

*B. tintinnabulum communis* L.

*B. improvisus gryphica* Mün.

*B. perforans* Brug.

*B. amphitrite* Darw.

*B. eburneus* Gould

*Pinnotheres pisum* Penn.

*Eupagurus Prideauxi* Leach

*Gammarus marinus* Leach

*Talitrus saltator* Mont.

*Libinia dubia*

*Uca pugnax*, *U. pugilator*

*Talorchestia longicornis* Say.

*Ampelisca spinipes*

## GENERA OF UNCERTAIN POSITION

*Nematoides fusiformis* Mingazzini

Type species

*Ganymedes anaspidis* Huxley

Type species

*Balanus perforatus*

*Pollicipes cornucopia*

*Anaspides tasmaniae* (Thomp.)

## UNNAMED SPECIES OF UNCERTAIN POSITION

[? *gammari* von Siebold]

[sp. Mawrodiadi]

*Gammarus pulex*

*Balanus amphitrite pallidus* Darw.

*B. amphitrite* Darw.

*B. eburneus* Gould

*Pollicipes polymerus* Say

*Cancer pagurus*

*Phronima* sp.

*Phronimella* sp.

*Hyale pontica* Rathke

*Nebalia serrata*

[? *valettei* Nussbaum]

[? *praemorsa* Diesing]

[? *clausii* Frenzel]

[? *nicaeae* Frenzel]

[sp. Minchin]

## Family DIDYMOPHYIDAE Léger 1892:105

Sporonts in associations of two or three. No septa in satellites.

## Genus DIDYMOPHYES Stein 1848:186

Characters of family. Epimerite a small pointed papilla, cyst dehiscence by simple rupture, spores ellipsoidal.

## DIDYMOPHYES LONGISSIMA (von Siebold) Frantzius

1839	<i>Gregarina longissima</i>	von Siebold	1839: 58
1848	<i>Didymophyes longissima</i>	Frantzius	1848: 196
1848	<i>Gregarina longissima</i>	Kölliker	1848: 34
1851	<i>Gregarina longissima</i>	Diesing	1851: 15
1859	<i>Gregarina longissima</i>	Diesing	1859: 735
1863	<i>Gregarina longissima</i>	Lankester	1863: 95
1886	<i>Gregarina longissima</i>	Plate	1886: 235
1895	<i>Gregarina</i> sp.	Pfeiffer	1895: 60
1899	<i>Didymophyes longissima</i>	Labbé	1899: 8
1903	<i>Didymophyes longissima</i>	Minchin	1903: 330, 331
1911	<i>Gregarina longissima</i>	Wellmer	1911: 119

Sporonts very elongate, cylindrical, vermiform in movements. Ratio LP : TL :: 1 : 30; WP : WD :: 1 : 1. Primate longer than satellite. Dimensions not given (Kölliker). Nucleus small, spherical, one large karyosome.

Intestine of *Gammarus pulex* von Siebold, *Orchestia littorea*.

Taken in Germany.

The species was first described by von Siebold, who also found another species in *Gammarus pulex*, typically like the Cephaloidophoridae in outline but regarded by him as another form of the same species.

Kölliker studied fresh material adding the data that associations exist of two or three elongate slender individuals arranged in single file and of two satellites attached to the posterior end of the primate. Kölliker recognized the possibility of a new species being involved in von Siebold's material and illustrates this as well as the two modifications mentioned in the type species.

The exclusion of the doubted form was also recognized by Diesing (1859).

Lankester (1863) regards all the following as synonyms:

*Gregarina longissima* Siebold

? *Gr. diffluens* Diesing

*Gr. millaria* Diesing (Actinocephalus Stein)

*Gr. putanea* Leuckart

*Gr. Gammari* Siebold (Didymophyes Stein)

His basis was the identity of the hosts only.

Plate found in the intestine and coelom of *Gammarus pulex* "band-formig" gregarines 255 $\mu$  in max. length, three or four attached together and regards them as belonging to the species in question.

Minchin (1903) questions the inclusion of the last named host as authentic.



Léger and Duboscq (1911) have described a new species, *Cephaloidophora maculata*, from *Gammarus marinus* which is identical with the aberrant species referred to above.

#### Family GREGARINIDAE Labbé 1899:9

Epimerite symmetrical, simple. Sporonts solitary or in association. Cysts with or without spore-ducts, spores symmetrical.

#### Genus URADIOPHORA Mercier 1912a

Intestinal parasites. Development extracellular. Epimerite an elongate papilla. Cysts without sporeducts. Spores spherical or sub-spherical, not united in chains, faint equatorial line. End portion of deutomerite of satellite greatly constricted. Associations of two sporonts.

#### URADIOPHORA CUENOTI (Mercier) Mercier Type Species

[Figure 63]

1911	<i>Cephaloidophora Cuenoti</i>	Mercier	1911: 51
1911	<i>Cephaloidophora Cuenoti</i>	Sokolow	1911: 286
1912	<i>Uradiophora Cuenoti</i>	Mercier	1912a: xli
1912	<i>Uradiophora Cuenoti</i>	Mercier	1912b; 177
1912	<i>Uradiophora Cuenoti</i>	Trégouboff	1912: lvi
1913	<i>Uradiophora Cuenoti</i>	Ellis	1913: 264

Characters of the genus. Syzygies of two sporonts, infrequently of three. Sporonts very elongate, cylindrical. Ratio LP:TL::1:20 (primit) 1:28 (satellite without appendage). WP:WD::1:1.9 to 1:2. Sporonts 700 $\mu$  in max. length. Nucleus sub-spherical. Epimerite an elongate papilla, persistent in sporonts. Deutomerite with small atrophied appendix. Nucleus in adults spherical, with one large karyosome; chromidial bodies frequently found in both protomerite and deutomerite. Cysts ovoidal, 38 to 44 $\mu$  in diam. Spores 4 $\mu$  in diam.

Intestine of *Atyaephyra Desmaresti* Millet.

Taken at Nancy, France.

#### Genus PYXINOIDES Trégouboff 1912

Intestinal parasites, extracellular in development. Epimerite a short style dilated in middle to form a globe with sixteen longitudinal grooves, the free upper end of the style being about 2 $\mu$  in length. Septum with small disc-shaped horizontal swelling in middle. Sporont ovoidal, nucleus large, one karyosome. Syzygies of two sporonts, the primit always larger. Cyst and spores unknown.

## PYXINOIDES BALANI (Kölliker) Trégouboff Type Species

[Figures 65, 82, 88]

1848	<i>Gregarina balani</i>	Kölliker	1848: 35
1848	<i>Stylorhynchus Balani</i>	Frantzius	1848: 195
1851	<i>Gregarina Balani</i>	Diesing	1851: 10
1859	<i>Gregarina Balani</i>	Diesing	1859: 728
1863	<i>Gregarina Balani</i>	Lankester	1863: 95
1899	<i>Gregarina balani</i>	Labbé	1899: 36
1903	" <i>Gregarina</i> " <i>balani</i>	Minchin	1903: 329
1912	<i>Pyxinoides balani</i>	Trégouboff	1912: liii

Sporonts associated in pairs, ovoidal to cylindrical. Max. length seen by Kölliker  $63\mu$ , by Trégouboff  $130\mu$  primite,  $60\mu$  satellite. Ratio LP : TL :: 1:1.3 to 1:3; WP : WD :: 1:1 to 1:1.4. Protomerite dome-shaped, slightly dilated below middle, terminating in a long cone upon which is surmounted an epimerite in the form of a short stylet dilated centrally into a bulb (Kölliker). Deep constriction at septum, deutomerite widest in middle. Nucleus larger, spherical with one karyosome.

Intestine of *Balanus pusillus* Ecker; *B. tintinnabulum* L. (Köll.), *B. amphitrite* Darw., *B. eburneus* Gould (Trég.).

Taken at Trieste, Cete, France.

Kölliker first described this species, although he credits "Professor Ecker" with having seen it before, evidently without placing it upon record.

Frantzius reasonably considered it a member of the genus *Stylorhynchus* from the character of the epimerite, which resembles that of a new genus *Bulbocephalus* Watson (1916) of the family *Stylocephalidae*.

The species was not described again until the time of Trégouboff, who contributes many new observations, assigning to it a new name, evidently ignorant of the earlier work, and creating for it a new genus, *Pyxinoides*.

From the beautiful drawing of Kölliker, of a cephalont, there can be no doubt that one and the same species is involved. He even shows in the tiny figure the longitudinal grooves in the bulb of the epimerite.

Members of the genus *Balanus* also harbor *Nematoides fusiformis*, very similar in some respects but yet regarded as a separate species. See discussion under that species.

## PYXINOIDES CTHAMALI (Léger and Duboscq) Trégouboff

[Figures 78 and 81]

1909	<i>Frenzelina cthamali</i>	Léger and Duboscq	1909a: 112, 114, 115
1911	<i>Frenzelina cthamali</i>	Sokolow	1911: 281
1912	<i>Pyxinoides cthamali</i>	Trégouboff	1912: lviii

Sporonts regularly cylindrical, primite  $230\mu$  in max. length, satellite  $170\mu$ . Ratio LP : TL :: 1 : 4.5; WP : WD :: 1. 1. Protomerite wid-

est below mid-region, with characteristic specialized crescentic zone at apex, with what appears to be a canal leading from apex a short distance into protomerite. Deutomerite cylindrical, blunt at posterior end. No constriction at septum. Nucleus ovoidal with one large karyosome. Development extracellular. Epimerite atypical for that of the genus, but still Pyxinia-like, a long style reaching in large trophozoites to base of the cell and having a large crenulated cup-like enlargement at its mid-point, the rim of the cup being turned away from the body of the gregarine.

Cysts spherical, 85 to 100 $\mu$  in diameter. Spores unknown.

Intestine of *Cthamalus stellatus* Ranzani.

Taken at Cette, France.

In the first mention of the species, Léger and Duboscq 1909:112, the spelling is given as *chtamali* and that of the host genus *chtamalus*, while on pp. 114 and 115 the spelling is *chthamali* and *chthamalus*. Trégouboff gives it for both parasite and host as *cthamaali* (us).

#### Family CEPHALOIDOPHORIDAE Kamm 1922

Intestinal parasites of Crustacea, development intracellular, early syzygies of two sporonts. Cysts without sporeducts, spores ovoidal with equatorial line. Entire life cycle passed within a single host.

#### DISCUSSION OF THE NEW FAMILY CEPHALOIDOPHORIDAE

The genus Cephaloidophora was created in 1908 by Mawrodiadi for intestinal parasites of the Crustacea. Léger and Duboscq in 1907 created a genus in all respects identical with the former genus naming it Frenzelina; but in 1911 they discovered that the name Frenzelina was preoccupied, so the name Cephaloidophora becomes the accepted genus designation.

The genus Frenzelina had been placed with the Gregarinidae because of the precocious association of sporonts in pairs; but there the similarities stop. Cephaloidophora was placed in the family Stenophoridae (Sokolow 1911:286) and it must be acknowledged that there are many characters in common with that family, including (a) intracellular development, (b) rudimentary epimerite, (c) spores ovoidal with equatorial line, (d) cysts without spore-ducts, (e) spores not united in chains. (A) is confined to these two groups alone, in both of which there is cell-destruction, all other known forms possessing extracellular trophozoitic stages without or with but little injury to the host. The only important variance in the two groups lies in the fact that the Cephaloidophoridae invariably form early syzygies of two individuals while the Stenophoridae as invariably do not. The shape of the body, usual shape and character of the nucleus and texture of the protoplasm are different in the two groups. For complications given below, the gregarines of the Crustacea should be considered apart from all others, at least until many of the knotty points



are cleared up by exhaustive researches. For these reasons I have raised the genus *Cephaloidophora* to a new family, *Cephaloidophoridae*.

Unlike other great groups of gregarines, the complete life-history of a crustacean parasite must be known before it can be assigned to a particular genus with a reasonable assurance of permanence; generally two out of three or four characters will determine the location of a gregarine. Unless the evolution of a sporozoite from the spore (*Cephaloidophoridae*) or from the cyst direct (*Aggregatidae*) is known and the intracellular development has been observed or proven to be absent, a crustacean parasite cannot be accurately placed. Léger and Duboscq, the closest students of the gregarines of the Crustacea, have removed many species hitherto classed as gregarines to the family *Aggregatidae*, now placed in the order *Coccidia*, because the sporozoites develop in the cyst without the intervention of spores. The sporogonic cycle of the *Aggregatidae* is passed in another host, a Cephalopod. Thus an alternation of hosts corresponds to an alternation of generations, the crab being eaten by the Cephalopod.

Another family of gregarines inhabiting Crustacea is the *POROSPORIDAE*, parasitic in Decapods only. These animals are very large, usually but not always solitary in the adult and are capable of forming cysts from a single individual. This raises the question that such cysts are schizogonic cysts and that the sporogonic stage, which possibly has not been seen, is passed in another host.

Léger and Duboscq (1911:lix) offer this hypothesis:

. . . si *Cephaloidophora* et *Porospora* ne tomberont pas en synonymie, *Porospora* représentant la schizogonie et *Cephaloidophora* la gamogonie d'un même cycle.

Trégouboff (1912) says, however:

Je suis convaincu que les *Cephaloidophora* effectuent leur cycle dans un seul hôte et présentent un seul type des germes.

Minchin (1912:340) says:

A character such as the power of multiplication by schizogony is clearly one of great adaptive importance in the life-history of a parasitic organism, and therefore not likely to be of classificatory value. The classification of the future will probably be one which divides all gregarines into *Cephalina* and *Acephalina*, and distributes the *Schizogregarines* (into which suborder the *Porosporidae* are now placed) amongst these two divisions.

I think the last statement holds the clue to the classification of these puzzling forms. Léger and Duboscq first placed two of their early forms *Cephaloidophora fossor* and *C. ocellata* among the *Aggregatidae*, finding only coelomic cysts. After more exhaustive researches they found a life-history typically that of the genus *Cephaloidophora*, and removed the species to this genus, considering that the coelomic cysts they had previously found belonged to different gregarines, of which nothing else was known. I feel certain the latter really belonged in the same life-cycle and that the power of producing coelomic cysts and their concomitant



sporozoites within the original host is one means the parasite has of "holding its own" in Nature and reproducing at an enormous rate upon certain occasions. This migration of the young gregarine through the intestinal epithelium and production of a cyst from a single individual resulting in schizogonic sporozoites may be due to a change of food in the host animal unadapted to the parasite's requirements, to sickness of the host, to a scarcity of food, to the time of the year, or to a natural phenomenon occurring at stated intervals in the economy of the organism itself. Or it may be due to some extraneous cause not mentioned.

I am convinced that all the gregarines in the Crustacea will again come under one family head and that the Aggregatidae, the oldest known group, will be restored to its position among the gregarines. The Porosporidae and Cephaloidophoridae will of necessity be dropped. But in the meantime, until much more work on the crustacean parasites shall have been done and complete life-histories become the rule rather than the exception, the present group headings must remain.

Type Genus CEPHALOIDOPHORA Mawrodiadi 1908: 101

Intestinal parasites of Crustacea. Characters of the family.

CEPHALOIDOPHORA CONFORMIS (Diesing) Léger and Duboscq

[Figures 66 and 75]

1787	Unnamed	Cavolini	1787: 169
1810	? Distome	Rudolphi	1810: 287
1819	? Distome	Rudolphi	1819: 197
1851	<i>Gregarina conformis</i>	Diesing	1851: 15
1859	<i>Gregarina conformis</i>	Diesing	1859: 735
1863	<i>Gregarina conformis</i>	Lankester	1863: 95
1885	<i>Gregarina conformis</i>	Frenzel	1885: 579
1899	<i>Aggregata conformis</i>	Labbé	1899: 6
1903	<i>Aggregata conformis</i>	Minchin	1903: 331
1907	<i>Frenzelina conformis</i>	Léger and Duboscq	1907: 773
1908	<i>Frenzelina conformis</i>	Léger and Duboscq	1908: 99
1909	<i>Frenzelina conformis</i>	Léger and Duboscq	1909: 733
1909	<i>Frenzelina conformis</i>	Léger and Duboscq	1909a: 113
1911	<i>Frenzelina conformis</i>	Sokolow	1911: 280
1911	<i>Cephaloidophora conformis</i>	Léger and Duboscq	1911: lix
1913	<i>Aggregata conformis</i>	Ellis	1913: 264

(Frenzel) Sporonts associated in pairs, not more than two, irregularly cylindrical, tapering slightly, well-rounded posteriorly. Often a slight shoulder exists. Protomerite broadly dome-shaped, slightly constricted

at septum. 400 to 500 $\mu$  in length. Ratio LP:TL::1:6 (primate) 1:8 (satellite). WP:WD::1:5. Protomerite clear with large chromidial inclusions and crescentic apical area. Deutomerite dense, nucleus not seen in vivo, spherical, one or more karyosomes.

Cysts 150 $\mu$  in diameter. Spores ellipsoidal with faint equatorial line, 6.4 by 5 $\mu$ .

Intestine and gastric caeca of *Pachygraspus marmoratus* Fabr. (*Cancer depressus*).

Taken at Cavaliere, France, Naples, etc.

This is recognized as the earliest known species of Gregarines. Redi in 1708 found a parasite in the crab *Cancer pagurus* but Léger and Duboscq (1908) say:

La courte description et les images que Redi (1708) donne des vers du *Cancer pagurus* ne peuvent s'appliquer aux Gregarines des Crustacés, dont la découverte revient à Cavolini, quoiqu'en aient pensé Diesing (1851) et Labbé (1899).

Cavolini in 1787 discovered in "*Cancer depressi*" a parasite which he did not name and which Rudolphi (1810 and 1819) placed among his "vermes generis dubii," suggesting that it may be a Distome.

Diesing (1851) named the parasite *Gregarina conformis*. In the same paper he named another species seen by the same earlier workers *Gregarina praemorsa*. Hence either species might with equal right be named the type species. Diesing (1859) remarks only "*Individua solitaria* (Cavolini)."

Frenzel studied the species at length and gives several figures. The above description is taken mostly from his work.

Léger and Duboscq studied it again and find in their specimens that the satellite is the longer, while the primate is short and relatively stouter. The nucleus in their specimens is subspherical to ovoidal. Dimensions of the two descriptions compare favorably, an association given by the later workers as 1050 $\mu$  in length, 400 $\mu$  for the primate, the former being 80 $\mu$  wide and the latter 40 $\mu$ . Ratios of drawing of the latter's work are as follows: LP:TL::1:9 (primate) 1:21 (satellite); WP:WD::1:1.5 to 1:1.2. Thus their specimens conform to the type.

In 1907 these workers report schizogonic stages encountered in the coelom. They also found sporogonic encystment in the intestine with cysts 150 $\mu$  in diameter found in the excrement and two sizes of spores, 6.4 by 5 $\mu$  and microspores 5 $\mu$  by 4.7 $\mu$ .

## CEPHALOIDOPHORA COMMUNIS Mawrodiadi Type Species

[Figure 77]

1890-1	No name	Solger	1890-1: 233
1899	<i>Gregarina</i> sp.	Labbé	1899: 36
1903	<i>Gregarina</i> sp.	Minchin	1903: 329
1908	<i>Cephaloidophora communis</i>	Mawrodiadi	1908: 101
1911	<i>Cephaloidophora communis</i>	Sokolow	1911: 286
1912	<i>Cephaloidophora communis</i>	Mercier	1912a: xli
1912	<i>Cephaloidophora communis</i>	Trégouboff	1912: liii

Sporonts 65-80 $\mu$  in length. Protomerite and deutomerite rounded. Associations in pairs, the primate the larger. Intracellular trophozoites found in intestinal epithelium and hepatic cells. A thickened hyalin crescentic area at apex of protomerite corresponding to a rudimentary epimerite. Ratio LP:TL::1:4; WP:WD:1:1.5. Cysts spherical. Spores with eight sporozoites, ovoidal, 4.5 by 4 $\mu$ , with faint equatorial line. Sporozoites subspherical

Hosts: *Balanus improvisus* Darw.; *B. improvisus gryphica* Münter; *B. tintinnabulum communis* L.; *B. perforans* Brug.; *B. amphitrite* Darw.; *B. eburneus* Gould.

Habitat: Intestine and caeca.

Taken at Odessa, Cete, France, etc.

The original description is in Russian and is not available. The above data is taken from Sokolow's translation and from Trégouboff's new observations upon live material.

Buddington (1910:470) gives a brief description of an unnamed species found in *Balanus eburneus* Gould, presumably at Woods Hole, Mass., merely stating the animal to be a polycystid gregarine of rapid movement, with a nucleus having five karyosomes and chromidial bodies in the protomerite. It is quite probable that he found the above species.

## CEPHALOIDOPHORA FOSSOR (Léger and Duboscq) Trégouboff

[Figure 79]

1901	<i>Aggregata coelomica</i>	Léger	1901: 1343
1903	<i>Aggregata coelomica</i>	Léger and Duboscq	1903: cxlvii
1907	<i>Frenzelina fossor</i>	Léger and Duboscq	1907: 774
1908	<i>Frenzelina fossor</i>	Léger and Duboscq	1908: 99
1909	<i>Frenzelina fossor</i>	Léger and Duboscq	1909a: 112, 114, 115
1911	<i>Frenzelina fossor</i>	Sokolow	1911: 280
1912	<i>Cephaloidophora fossor</i>	Trégouboff	1912: lv
1912	<i>Cephaloidophora fossor</i>	Mercier	1912: xlv

Sporonts 150 $\mu$  in length. Ratio LP:TL::1:3 to 1:4; WP:WD::1:1.1. Sporonts obese, primate larger than satellite. Protomerite of primate broadly dome-shaped, twice as broad as high, with cres-



cent at anterior end and an apparent pore at the apex. Very slight constriction at the septum. Deutomerite ovoidal, broadly rounded at the distal end. Nucleus apparently ovoidal, situated near septum. Satellite more nearly cylindrical than primate.

Intracellular stage noted.

Intestine, coelom, and "sub-epithelium" of *Pinnotheres pisum* Penn.

In the first paper above, Léger reports finding coelomic schizogonic cysts  $150\mu$  in diameter which produce sporozoites directly.

Léger and Duboscq (1907) conclude that the two types of cysts encountered respectively in the coelom and alimentary tract represent different species of parasites, only one type of sporont having been seen, however. They have found no other stages of the coelomic gregarine except the cysts and contained sporozoites and have found all the stages in the life-history of the intestinal parasite. I am convinced that but one species is involved producing two kinds of cysts depending on conditions not yet determined. I am not ready, however, to remove any of the species now placed to another position. Much more work is needed upon crustacean gregarines and parasites placed elsewhere before any species can be assigned positions with a fair degree of permanence.

#### CEPHALOIDOPHORA OCELLATA (Léger and Duboscq) Kamm

[Figure 80

1903	<i>Aggregata vagans</i>	Léger and Duboscq	1903: cxlvii
1907	<i>Frenzelina ocellata</i>	Léger and Duboscq	1907: 774
1908	<i>Frenzelina ocellata</i>	Léger and Duboscq	1908: 99
1909	<i>Frenzelina ocellata</i>	Léger and Duboscq	1909a: 112, 114, 115
1911	<i>Frenzelina ocellata</i>	Sokolow	1911: 280-1
1922	<i>Cephaloidophora ocellata</i>	Kamm	1922 (this paper)

Sporonts in pairs, elongate cylindrical,  $200\mu$  in maximum length. Primate the larger. Ratio LP:TL::1:6 to 1:9; WP:WD::1:0.9. Protomerite widest anterior to the mid-region with two large corpuscles resembling eyes in both primate and satellite. A flattened cone projects at the anterior end. Slight constriction at septum. Deutomerite widest at shoulder, tapering from thence gradually and terminating in a broadly rounded end. Nucleus ovoidal to rectangular, situated at or above mid-region of deutomerite.

Intestine of *Eupagurus Prideauxi* Leach.

Taken at Banyuls, France.

This species was first described as *Aggregata vagans* and shown to exist during the sporont stage in the intestine but to be able to pass while comparatively large in size through the epithelium into the coelom. A single individual here swells, its protoplasm changes in character, and it finally becomes a schizogonic cyst  $150\mu$  in diameter in which are produced sporozoites directly, as in the family Aggregatidae.



Typical sporont cysts are also noted in the excrement from the alimentary tract.

The authors think that the two kinds of sporozoites represent different species of parasites, the sporogonic representing the new species, *Frenzelina ocellata*. I am of the opinion that but one species is involved. See discussion under *Cephaloidophora fossor* and also Discussion of the New Family Cephaloidophoridae, at the beginning of Crustacean Parasites.

#### CEPHALOIDOPHORA MACULATA Léger and Duboscq

[Figure 68]

1911	<i>Cephaloidophora maculata</i>	Léger and Duboscq	1911 : lix
1912	<i>Cephaloidophora maculata</i>	Trégouboff	1912 : liv
1912	<i>Cephaloidophora maculata</i>	Mercier	1912a: xliii

Sporonts small, ovoidal, maximum length  $80\mu$ . Ratio LP : TL :: 1 : 4 to 5; WP : WD :: 1 : 1.5 to 2. Cytoplasm yellowish in deutomerite, clear in protomerite. Spherical chromidial bodies in protomerite. Nucleus small, spherical, one karyosome. Characteristic crescentic apical area in protomerite. Cysts spherical,  $100\mu$  in diameter. Spores spherical to subspherical,  $4\mu$  in diameter, with equatorial line. Intracellular stage observed.

Intestine of *Gammarus marinus* Leach.

Taken at Roscoff, France.

#### CEPHALOIDOPHORA TALITRI Mercier

[Figure 86]

1912	<i>Cephaloidophora talitri</i>	Mercier	1912: 38
1912	<i>Cephaloidophora talitri</i>	Mercier	1912a: xliv
1912	<i>Cephaloidophora talitri</i>	Trégouboff	1912: lv

Sporonts in pairs, primate the larger, ovoidal, average length  $40\mu$ . Ratio LP : TL :: trophozoites 1 : 4.5 to 6; WP : WD :: 1 : 1.2 to 2. Protomerite dome-shaped with rudimentary epimeritic area at apex. Slight constriction at septum. Deutomerite broadly ovoidal, nucleus spherical with one large karyosome. Intracellular stage noted.

Cyst and spores unknown.

Intestine of *Talitrus saltator* Mont.

Taken at Roscoff, France.

#### CEPHALOIDOPHORA OLIVIA (Watson) Kamm

[Figure 83]

1912	<i>Frenzelina olivia</i>	Watson	1916: 133
1922	<i>Cephaloidophora olivia</i>	Kamm	1922 (this paper)

Sporonts in pairs, max. length association  $218\mu$ , ellipsoidal, largest sporont  $118$  by  $36\mu$ . Ratio LP : TL :: 1 : 5. WP : WD :: 1 : 1.3.

Protomerite dome-shaped, constriction at septum slight, papillate area at apex of protomerite orange in color. Deutomerite long-ovoidal. Nucleus spherical, one karyosome. Cysts spherical, 60 $\mu$ . Spores unknown.

Intestine of *Libinia dubia*.

Taken at Cold Spring Harbor, Long Island.

#### CEPHALOIDOPHORA NIGROFUSCA (Watson) Kamm

[Figure 84]

1912 <i>Frenzelina nigrofusca</i>	Watson	1916: 134
1922 <i>Cephaloidophora nigrofusca</i>	Kamm	1922 (this paper)

Sporonts stout-bodied, ovoidal to rectangular, maximum size 125 $\mu$  by 75 $\mu$ . LP:TL::1:4; WP:WD::1:1.5. Protomerite broadly dome-shaped with characteristic papillate apical area. Slight constriction at septum. Deutomerite regularly cylindrical, broadly-rounded at posterior end. Protoplasm very dense. Nucleus small, spherical with one or two karyosomes.

Cysts and spores unknown.

Hosts: *Uca pugnax*, *Uca pugilator*. Intestine.

Taken at Cold Spring Harbor, Long Island.

#### CEPHALOIDOPHORA DELPHINIA (Watson) Kamm

[Figure 85]

1916 <i>Frenzelina delphinia</i>	Watson	1916: 29
1922 <i>Cephaloidophora delphinia</i>	Kamm	1922 (this paper)

Sporonts ovoidal, maximum length association 215 $\mu$ , largest sporont 115 by 64 $\mu$ . Ratio LP:TL::1:4; WP:WD::1:1.5. Protomerite irregularly dome-shaped, dilated medianly. Papillated apex. Very slight constriction at septum. Deutomerite ovoidal. Nucleus spherical, one karyosome.

Cysts spherical, 80 $\mu$ . Spores unknown.

Intracellular stage noted.

Intestine of *Talorchestia longicornis* Say.

Taken at Cold Spring Harbor, Long Island.

#### CEPHALOIDOPHORA AMPELISCA (Nowlin and Smith) Kamm

[Figure 71]

1917 <i>Frenzelina ampelisc</i>	Nowlin and Smith	1917: 83
1920 <i>Cephaloidophora ampelisc</i>	Kamm	1922 (this paper)

Sporonts elongate cylindrical, 62 $\mu$  by 15 $\mu$  in maximum dimensions. Sporonts in pairs. Ratio LP:TL::1:6 to 1:9; WP:WD::1:1. Protomerite broadly dome-shaped, dilated in middle, more or less constricted at septum and possessing a rudimentary epimerite or broad

apical papilla. Several chromidial bodies in protomerite. Deutomerite cylindrical, blunt at posterior end. Nucleus spherical with one or more karyosomes.

Intracellular development noted.

Intestine and hepatic caeca of *Ampelisca spinipes*.

Taken at Woods Hole, Mass.

#### Genera of Uncertain Position

#### NEMATOIDES Mingazzini 1891 2nd sem.: 233

Dicystid, no septum in sporonts. Epimerite forked, at apex of a long neck. "Corpo allungato fusiforme, aguzzo ad entrambi gli apici. Cuticola liscia."

#### NEMATOIDES FUSIFORMIS Mingazzini Type Species

1891	<i>Nematoides fusiformis</i>	Mingazzini	1891: 2nd sem. 233
1899	<i>Nematoides fusiformis</i>	Labbé	1899: 34
1903	<i>Nematoides fusiformis</i>	Minchin	1903: 203, 329, 331

Characters of the genus. "Trophozoite vermiform, without septum. Epimerite in form of a fork or pair of pincers, borne on an elongated neck." Minchin.

Intestine of *Balanus perforatus*, *Pollicipes cornucopia*.

*Balanus* sp. also harbor *Cephaloidophora communis* Mawr. and *Pyxinoides balani* (Kölliker) Trégouboff.

Mingazzini says the new species above is the *Gregarina balani* of Kölliker. But the cephalont depicted by Kölliker corresponds in every particular with that of an early cephalont of *Pyxinoides balani*. See discussion under that species.

If, however, the fully developed epimerites of the two species, *Pyxinoides balani* and *Nematoides fusiformis* are considered, they are suspiciously similar. Labbé emends the original description of the latter thus:

Epim. en forme de fourche ou de pince,

séparé par un col allongé du reste du corps.

The only character, then, in which the two species differ is this: The latter possesses no septum in the sporont and is in appearance a Monocystid, while the former has a complete septum in all stages except the very earliest. Exhaustive researches may contribute something upon this point and prove the two species identical.

Below is the original description of the species:

Cercando nell'intestino del *Balanus perforatus* la *Gregarina balani* der Kölliker che è una policistidea, ho trovato invece una monocistidea appartenente a questo gruppo di gregarine vermiformi. È piuttosto lunga, ha la membrana intieramente liscia, un nucleo ovale al centro con un nucleolo. Sembra assai rara. L'apice anteriore, troncato, termina con una specie di ventosa, il posteriore invece è affatto puntuto. Nell'apice anteriore vi è un po'di metaplasma, nel resto vi ha l'endoplasma.

## GANYMEDES Huxley 1910:55

A possible fixation organ at interior end, consisting of a motile stalked sphere. Cup at posterior end which fits into ball of a satellite. No septum, no true epimerite. Typical gregarinoid encystment, cysts spherical. Alimentary tract of Crustacea.

Huxley offers the hypothesis that this gregarine lies between the polycystids and the monocystids and creates for it a new family, Ganymedidae. Since his studies were made only upon fixed material and all characters of this very unusual parasite are unknown, I think the rank of a new family is hardly justifiable and prefer to consider it among the Genera of Uncertain Position.

## GANYMEDES ANASPIDIS Huxley Type Species

[Figure 89]

1910	<i>Ganymedes anaspidis</i>	Huxley	1910: 155
1913	<i>Ganymedes anaspidis</i>	Ellis	1913: 264

Characters of the genus. Sporonts in pairs, elongate cylindrical, maximum length  $200\mu$ , width  $120\mu$ . Average size  $250\mu$  to  $300\mu$  by  $17\mu$  to  $20\mu$ . Nucleus large, ellipsoidal, one large karyosome. Cysts spherical,  $100\mu$  in diameter.

Anterior end of protomerite a "distinct stalked sphere," 8 to  $10\mu$  across. Protoplasm of anterior end highly specialized, posterior end a socket into which fits the "ball" of another individual, during the associative period.

Intestine and pyloric caeca of *Anaspides tasmaniae* (Thompson).

Taken on the Island of Tasmania.

## Species of Uncertain Position

[? *gammari* von Siebold]

1839	<i>Gregarina gammari</i>	von Siebold	1839: ?
1848	<i>Gregarina Gammari</i> ?	Frantzius	1848: 196
1848	? <i>Gregarina longissima</i>	Köl liker	1848: 35
1859	<i>Gregarina Gammari</i>	Diesing	1859: 735
1863	<i>Gregarina longissima</i>	Lankester	1863: 95
1886	<i>Gregarina Gammari</i>	Plate	1886: 236
1895	<i>Gregarina</i> sp.	Pfeiffer	1895: 60
1899	<i>Gregarina</i> sp.	Labbé	1899: 36
1903	<i>Gregarina</i> sp.	Minchin	1903: 330

Epimerite present. Sporonts  $425\mu$  in length, long-ovoidal.

Intestine and ? coelom of *Gammarus pulex*.

von Siebold described *Didymophyes longissima* from the same host, considering it a second form of the same species. In the same paper,



however, he described the above species from the same host, overlapping his first observations with two names.

Diesing (1859) refers to this species thus:

Receptaculum globosum. Corpus ovoideum receptaculo duplo longius. Longit . . . crassit . . .

He regards it as synonymous with the specimens seen by von Siebold and described by Kölliker as follows:

Neben dieser Gregarine fand v. Siebold in *Gammarus pulex* noch eine andere Form (Fig. 29c), von der es zweifelhaft bleibt, ob sie als Entwicklungsform zu der *Gr. longissima* zu rechnen ist oder nicht.

Kölliker's figure obviously represents an entirely different species which seems to correspond to one mentioned later in this discussion.

Lankester (1863) regards these as synonymous:

*Gregarina longissima* Sieb., *Gr. diffluens* Dies., *Gr. millaria* Dies., *Gr. putanea* Leuckart, *Gr. Gammari* Sieb.

Plate (1886) found in the intestine of *Gammarus pulex* two polycystid gregarines. One is small, elongate cylindrical, 255 in length, the other long-ovoidal, 425 $\mu$  in length. The one seems to correspond with *Didymophyes longissima* and the other with *Gregarina gammari*.

This species agrees in form and proportions with *Cephaloidophora maculata* from *Gammarus marinus* but sporonts of the present species attain 425 $\mu$  in length while those of the former reach only 80 $\mu$ .

Two species described by Diesing (1851:7) both from *Gammarus pulex* are sufficiently alike to be considered synonymous. No detailed description of the species (? *Gammari* von Sieb.) is extant and so they cannot be compared in minutae with the present species, but since all three are found in the same host they should obviously be considered together under the oldest name. These species are mentioned below

1851 *Gregarina millaria* Diesing 1851: 7

1859 *Gregarina millaria* Diesing 1859:731

Proboscis cylindrica gracilis, apice obtuse conica, uncinulorum seriebus 10-20. Receptaculum subglobosum papillosum. Corpus ellipticum turgidum receptaculo triplo longius, laete auranticum. Longit.  $\frac{1}{2}$ ''', crassit. . .

Hosts: *Gammarus pulex*, *Astacus fluviatilis*. Intestine.

1851 *Gregarina diffluens* Diesing 1851: 7

1859 *Gregarina diffluens* Diesing 1859: 731

Proboscis cylindrica brevis gracilis, apice longe conica obtusa, uncinulorum seriebus 10-20. Receptaculum subglobosum papillosum. Corpus oblongum per intervalla coarctatum postice rotundatum, saturate auricatum, facillime diffluens. Longit. 1''''; crassit. . .

Host: *Gammarus pulex*.

[? sp. Mawrodiadi]

1908	No name	Mawrodiadi	1908: 101
1911	<i>Gregarina</i> sp.	Sokolow	1911: 287
1912	No name	Trégouboff	1912: lviii

Sporont 130-140 $\mu$  in length, same general form as *Pyxinooides balani* (Kölliker) Trégouboff, but with a long epimerite which penetrates to the muscular layer.

. . . la grégarine possède un long épimérite, qui traverse tout le tissu épithélial, s'accolle à la gaine musculaire sous-jacente et la suce. (Quoted by Trégouboff from Mawrodiadi.)

Trégouboff adds:

Il est impossible de juger même de la parenté entre ces deux Grégarines étant donné la défec-tuosité de la description qui d'ailleurs tient toute dans les quelques mots cités plus haut.

Intestine of *Balanus amphitrite pallidus* Darw., *B. amphitrite* Darw., *B. eburneus* Gould.

Taken in the Black Sea.

[? valettei Nussbaum]

1890	<i>Gregarina valettei</i>	Nussbaum	1890: 156
1899	<i>Gregarina valettei</i>	Labbé	1899: 36
1903	" <i>Gregarina</i> " <i>valettei</i>	Minchin	1903: 331
1912	<i>Gregarina valettei</i>	Trégouboff	1912: lvii

Epimerite a simple stylet. Sporont 58 $\mu$  in length.

Intestine of *Pollicipes polymerus* Sow.

Taken in California.

Trégouboff concludes

. . . cette Gregarine, . . . n'est certainement pas une *Gregarina sensu stricto*.

[? praemorsa Diesing]

1684	?	Redi	1684: 183
1729	?	Redi	1729: 270
1810	Distome or Monostome?	Rudolphi	1810: 287
1819	Distome or Monostome?	Rudolphi	1819: 197
1851	<i>Gregarina praemorsa</i>	Diesing	1851: 287
1859	<i>Gregarina praemorsa</i>	Diesing	1859: 735
1863	<i>Gregarina praemorsa</i>	Lankester	1863: 95
1899	<i>Aggregata praemorsa</i>	Labbé	1899: 6
1903	<i>Aggregata praemorsa</i>	Minchin	1903: 329
1908	<i>Frenzelina praemorsa</i>	Léger and Duboscq	1908: 99
1909	<i>Frenzelina praemorsa</i>	Léger and Duboscq	1909a: 112
1911	<i>Frenzelina praemorsa</i>	Sokolow	1911: 280
1922	<i>Cephaloidophora</i> (?) <i>praemorsa</i>	Kamm	1922 (this paper)

Intestine and "ovarian appendage" of *Cancer pagurus* L. (*Platycarcinus* (Lankester)).

The first reference in literature to what may possibly have been a gregarine was that of Redi in 1684, who found in the "vesicular ovariorum" of *Cancer paguri* a parasite which Rudolphi (1810, 1819) refers to as a possible Distome or Monostome, and places in a list of "Vermes generis dubii."

Diesing (1851) named the species *Gregarina praemorsa* from the originally observed material and contributes no new observations. In 1859 he merely reports "Individua solitaria (Redi)."

As stated under *Cephaloidophora conformis*, Léger and Duboscq (1908) do not credit Redi's observations as referring to authentic gregarines but give to Calvolini (1787) the honor of having first seen and recorded undoubted specimens of this group. Rudolphi does not mention Cavolini in connection with the present species, however.

Léger and Duboscq (1908 and 1909a) merely mention the species by name in a list with this heading:

Le genre Frenzelina comprend ainsi actuellement les especes suivantes:

Sokolow lists it with the authentic species of the genus Frenzelina, not with a group of uncertain species.

Thus there is no record of positive data concerning the actual existence of this parasite as a gregarine. No description or drawing is extant. It is remarkable that the mere reference has held its place in literature for over two hundred years.

[? clausii Frenzel]

[Figure 69]

1879 ?	Claus	1879: 78
1885 <i>Gregarina Clausii</i>	Frenzel	1885: 575
1899 <i>Gregarina clausi</i>	Labbé	1899: 37
1903 " <i>Gregarina</i> " <i>clausi</i>	Minchin	1903: 331

Sporonts solitary, ovoidal,  $100\mu$  in maximum length. Ratio LP: TL :: 1:5.5; WP:WD :: 1:1.5. Epimerite unknown. Protomerite domeshaped, striated longitudinally. Deutomerite widest at shoulder, tapering to a rounded point. No constriction at septum. Chromidial bodies in protomerite. Nucleus spherical.

Solitary encystment within two thick hyalin cyst-walls. Cysts and spores not described.

Intestine of *Phronima* sp., *Phronimella* sp.

Taken at Naples.

The position of this species cannot be determined from the known data. Inclusion within the Cephaloidophoridae is doubtful from the solitary encystment.

[? nicaeae Frenzel]

[Figure 70]

1885 <i>Gregarina Nicaeae</i>	Frenzel	1885: 578
1899 <i>Aggregata nicaeae</i>	Labbé	1899: 6
1903 <i>Aggregata nicaeae</i>	Minchin	1903: 330

Sporonts associated in pairs. Length 60 $\mu$ . Ratio LP:TL::1:3 to 4; WP:WD::1:1. Protomerite dome-shaped, deutomerite tapering to a blunt point. No constriction at septum. Nucleus large, spherical, 15 $\mu$  in diameter.

Cyst and spores unknown.

Intestine of *Hyale pontica* Rathke (*Nicaea Nilsonii*).

Taken at Naples.

There is an equal possibility of this species belonging with the Cephaloidophoridae and with the Aggregatidae from the characters recorded. The exact position can only be determined after cyst and spores (or their absence) are demonstrated.

[? sp. Minchin]

1903	Septate Gregarine	Minchin	1903: 330
	"Original observation."		
	Intestine of <i>Nebalia serrata</i> .		
	No comment whatever is offered concerning this parasite.		

#### LIST OF SPECIES FOUND IN THE CLASS ACERATA

PARASITE	Host
<b>ACTINOCEPHALIDAE</b>	
<i>Anthorhynchus sophiae</i> (Schneider) Labbé	<i>Phalangius opilio</i>
Type species	
<i>Sciadophora phalangii</i> (Léger) Labbé	<i>Phalangium crassum</i>
Type species	<i>P. cornutum</i>
<i>Sciadophora fissidens</i> (Rössler) Labbé	<i>Opilio grossipes</i> Herbst.
<i>Sciadophora caudatus</i> (Rössler) Kamm	<i>Phalangidae</i> sp.
<i>Sciadophora goronowitschi</i> (Johansen) Labbé	<i>Phalangium opilio</i>
<b>ACANTHOSPORIDAE</b>	
<i>Acanthospora repelini</i> Léger	<i>Phalangium cornutum</i>
	<i>P. opilio</i>
<b>UNCERTAIN SPECIES</b>	
[? <i>Wellmer</i> ]	<i>Oribata geniculata</i> (L.)
Not named Sokolow]	<i>Scorpio indicus</i>

#### Family ACTINOCEPHALIDAE Léger 1892:166

Sporonts solitary, epimerites complex and varied. Cyst dehiscence by simple rupture, spores irregular, biconical, or cylindro-biconical.

Genus ANTHORHYNCHUS Schneider 1887:69, emend Labbé 1899:19

Epimerite a large flattened and fluted button, spores ovoidal, knobbed at sides, united in chains laterally.



## ANTHORHYNCHUS SOPHIAE (Schneider) Labbé Type Species

[Figures 58, 108]

1887	<i>Anthocephalus Sophiae</i>	Schneider	1887: 69
1897	<i>Anthocephalus Sophiae</i>	Léger	1897: 11
1899	<i>Anthorhynchus Sophiae</i>	Labbé	1899: 19
1903	<i>Anthorhynchus Sophiae</i>	Minchin	1903: 199, 338
1913	<i>Anthorhynchus Sophiae</i>	Ellis	1913: 279

Sporonts solitary, obese. Maximum length 2 mm. Width protomerite  $330\mu$ , deutomerite  $600\mu$ . Ratio LP:TL::1:11 (without epimerite); WP:WD::1.2. Protomerite small, flattened, three times as wide as high, no constriction at septum. Deutomerite conoidal, widest just below septum, tapering thence and ending in a broad blunt extremity. Epimerite a series of short blunt digitiform processes united laterally and curved inward to form a broad flattened corona. Epimerite  $200\mu$  high. Nucleus not described.

Spores 6.9 by  $4.6\mu$ , broad, biconical, extruded in chains laterally attached.

Intestine of *Phalangium opilio*.

Taken at Poitiers, France.

Genus SCIADOPHORA Léger 1897: 36, emend Labbé 1899: 18

Epimerite a large flattened centrally indented papilla with a crenulate periphery. Protomerite with numerous backwardly directed leaf-like processes arranged vertically, each sharply pointed at its posterior extremity.

## SCIADOPHORA PHALANGII (Léger) Labbé Type Species

[Figures 59, 60, 62, and 106]

1897	<i>Lycosella Phalangii</i>	Léger	1897: 12, 36
1899	<i>Sciadophora phalangii</i>	Labbé	1899: 18
1903	<i>Sciadophora phalangii</i>	Minchin	1903: 199, 338
1911	<i>Sciadophora phalangii</i>	Wellmer	1911: 127
1913	<i>Sciadophora phalangii</i>	Ellis	1913: 280

Sporonts solitary, very elongate, up to 2.5 mm., one of the largest known species. Width not given. Ratio LP:TL::1:12; WP:WD::1.3:1. Protomerite broadly conical at apex with 15 or 16 vertical lamillar plates starting below the apical cone recurving backward and terminating in sharp hooks. The whole bears a resemblance to an umbrella. Deep constriction at septum. Deutomerite widest at shoulder, tapering to a very long slender acuminate extremity. Epimerite a large

nearly sessile papilla indented in middle and crenulate on periphery. Nucleus ovoidal, nearly spherical, with many karyosomes.

Cysts spherical,  $\frac{1}{2}$  mm., dehiscence by simple rupture, spores biconical but rounded off at poles. Unique.  $9 \times 5\mu$ .

Intestine and caeca of *Phalangium crassum*, *P. cornutum*, *Opilio grossipes* Herbst.

Taken in Provence, France and East Prussia.

Two species have been described previous to this one and considered by Léger as synonymous; I have, however, not considered them so. They are incompletely described but quite different from the type species and because of the regularity of the digitiform bifurcate processes may not belong in the genus. This is what Léger says concerning the species:

. . . sans rien préjuger des espèces observées par M. Johansen et M. Rössler, je donne à celle que j'ai étudiée le nom spécifique de *Lycosella phalangii* qui indique son origine. Il ne paraît pas douteux cependant que, d'après leurs caractères morphologiques, les deux grégaires signalées par ces auteurs appartiennent au genre *Lycosella* et soient des espèces très voisines de celle que je décris dans ce travail, c'est ce que l'étude complète de leur cycle viendra nous confirmer un jour ou l'autre.

#### SCIADOPHORA FISSIDENS (Rössler) Labbé

[Figures 110 and 111]

1882	<i>Actinocephalus fissidens</i>	Rössler	1882: 700
1897	<i>Lycosella Phalangii</i>	Léger	1897: 12, 36
1899	<i>Sciadophora fissidens</i>	Labbé	1899: 18
1903	<i>Sciadophora fissidens</i>	Minchin	1903: 338

Sporonts solitary, 2 to 3 mm. in length. Ratio LP : TL :: 1 : 8; WP : WD :: 1 : 1.5. The protomerite is broadly dome-shaped, at the mid-region there is developed a corona of processes directed gently backward in two rows, the upper consisting of twelve long sharp spines, the lower of twelve broad plates widest at the middle and bifurcate at the ends, superficially resembling a lobster's claw. These are arranged alternately with the spines of the upper row. (Fig. 111). Deutomerite widest at shoulder, tapering gently backward, the posterior third, however, being a very much narrowed cylinder. Nucleus small, spherical.

Intestine and caeca of *Phalangidae* sp.

Taken at Freiburg, Germany.

This peculiar parasite in appearance is very unlike the type species, (Cf. Figs. 62 and 110) but because the crenulations are a part of the protomerite and not an epimerite, must be placed in this genus, or in a yet undescribed genus very similar. The complete life-history remaining unsolved, the species is placed here tentatively.

Rössler describes the peculiar protuberances thus:

. . . zeigt am Kopf zwölf gespaltene Hakenpaare und zwischen je zweien dieser Paare einen einfachen, stachelförmigen Dorn.

## SCIADOPHORA CAUDATUS (Rössler) Kamm

[Figures 112 and 113]

1882	<i>Stylorhynchus caudatus</i>	Rössler	1882: 700
1899	<i>Stylorhynchus caudatus</i>	Labbé	1899: 33
1903	<i>Stylorhynchus caudatus</i>	Minchin	1903: 338
1913	<i>Stylocephalus caudatus</i>	Ellis	1913: 338
1922	<i>Sciadophora caudatus</i>	Kamm	1922 (this paper)

Sporonts solitary, 2 to 2.5 mm. with a long "tail-process" 2 to 3 mm. in addition. This makes the species the longest known gregarine. Body similar in shape to *S. fissidens* except for the tail. The protomerite is situated upon a short neck with a dome-shaped top and a corona of twelve digitiform processes at the mid-region. Nucleus spherical.

Intestine and caeca of Phalangidae sp.

Taken at Freiburg, Germany.

This species and the preceding one are differentiated by the character of the protomeritic corona. Cf. Figs. 111 and 113. It is evident that they belong to the same genus, for the corona of each is a part of the protomerite rather than of an epimerite. Rössler considers the fact that this species possesses a long neck upon which is superimposed the protomerite sufficient evidence to place it in the genus *Stylocephalus*, but the coronae are so similar and the host identical—the two found in the same intestines—leads one to suspect that the two forms may represent parts of a single life-history. Further investigations are, however, necessary to establish this statement or refute it.

Rössler says concerning the species:

... besitzt einen gestielten Kopf, der mit zwölf Erhebungen oder Leisten versehen ist, die über den Rand desselben hinausragen und sich theilen. Diese Form ist ausserdem mit einem dünnen, schwanzartigen Anhang versehen der durch keine Scheidewand von dem eigentlichen Körper getrennt ist, jedoch auch keine einspringenden Konturen zeigt, die auf einen verstümmelten Zustand schliessen liessen.

## SCIADOPHORA GORONOWITSCHI (Johansen) Labbé

[Figures 104 and 105]

1894	<i>Actinocephalus Goronowitschi</i>	Johansen	1894: 140
1897	<i>Lycosella Phalangii</i>	Léger	1897: 11, 36
1899	<i>Sciadophora goronowitschi</i>	Labbé	1899: 18
1903	<i>Sciadophora goronowitschi</i>	Minchin	1903: 338

No dimensions or complete figure are given. Johansen describes the peculiar parasite thus:

... näher zum Deutomerit gelegenen Äquator eine Reihe von Häckchen und Dörnchen zur Befestigung des Parasiten an dem Gewebe der Phalangide dient.

His meagre illustration, Fig. 105, indicates a bifurcation of the processes, as in the species found by Rössler.

Maximum length 5 mm. This length is reached only by the species just preceding, the two being the longest known species of gregarines.

Intestine of *Phalangium opilio*.

Taken at Toms, Russia.

Léger also found *Acanthospora repelini* in his material.

#### Family ACANTHOSPORIDAE Léger 1892: 167

Sporonts solitary. Epimerite simple or appendicular. Dehiscence by simple rupture. Spores with equatorial and polar spines.

#### Genus ACANTHOSPORA Léger 1892: 167

Epimerite a simple large conical papilla on a short neck. Spores biconical or ovoidal with a row of equatorial spines and a tuft of four spines at each pole.

#### ACANTHOSPORA REPELINI Léger

[Figures 57 and 107]

1897	<i>Acanthospora Repelini</i>	Léger	1897: 13, 42
1899	<i>Acanthospora repelini</i>	Labbé	1899: 28
1903	<i>Acanthospora repelini</i>	Minchin	1903: 338
1911	<i>Acanthospora repelini</i>	Wellmer	1911: 139

Sporonts solitary, obese. Maximum length 1 mm., width 250 $\mu$ . Ratio LP : TL :: 1 : 4 (without epimerite); WP : WD :: 1 : 1.2. Proto-merite dome-shaped, deeply constricted at septum. Deutomerite widest in anterior third, tapering irregularly to a sharp point. Epimerite a broad flattened papilla indented in the middle and crenulate along the margin. Nucleus spherical, one karyosome.

Cysts spherical, 500 $\mu$ , dehiscence by simple rupture. Spores 13 by 4.8 $\mu$ , biconical, spines at apices and equator.

Intestine of *Opilio grossipes* Herbst, *Phalangium cornutum*, and *P. opilio*.

Taken in Tourraine, France, and in East Prussia.

This species was found in association with *Sciadophora phalangii* by Léger. There is no possibility of confusion, however, in the two species.

The epimerite of this species does not conform closely to that of the type, *A. pileata* (Léger, 1892: 115).

#### Uncertain Species

[? Wellmer]

1911	<i>Gregarina</i> sp.	Wellmer	1911: 148
Intestine of <i>Oribata geniculata</i> (L.). Taken in East Prussia.			
There are no data whatever concerning this gregarine form.			



		[? Sokolow]	
		[Figure 109]	
1908	Not named	Sokolow	1908: 500
1911	Not named	Sokolow	1911: 295
33 $\mu$ in length. Nucleus spherical, 3 $\mu$ . Seen in copulation.			
Host: <i>Scorpio indicus</i> .			
No other data are given concerning this gregarine form.			

## SPECIES FOUND IN THE CLASS MALACOPODA

## SPECIES OF DOUBTFUL POSITION

[? Moseley]		<i>Peripatus capensis</i> Grube	
	[? Moseley]		
1874	" <i>Gregarinae</i> "	Moseley	1874: 762
1899	<i>Gregarina</i> sp.	Labbé	1899: 37
1903	<i>Gregarina</i> sp.	Minchin	1903: 331

The only data which exist concerning this parasite are the following:

Some very small encysted *Gregarinae* were found in the stomachs of all the specimens examined.

Host: *Peripatus capensis* Grube.

Taken in Equatorial Africa.

One might wish that more data existed concerning the type of gregarine which inhabit this intermediate host. Theoretically, it should be a form intermediate between the family Polyrrhabdinidae and the true Cephaline Gregarines.

LIST OF SPECIES FOUND IN THE ORDER THYSANURA OF THE CLASS  
HEXAPODA

PARASITE	Host
GREGARINIDAE	
<i>Gregarina lagenoides</i> (Léger) Labbé	<i>Lepisma saccharina</i> L.
SPECIES OF DOUBTFUL POSITION	
? <i>Gregarina podurae</i> (Léger) Labbé	<i>Podura villosa</i>
<i>Gregarina</i> sp. Wellmer	<i>Sminthurus fuscus</i> L.

Family GREGARINIDAE Labbé 1899: 9

Genus GREGARINA Dufour 1828: 366

Sporonts in pairs, epimerite a small sessile knob or cone. Spores barrel-shaped to cylindrical. Cysts with spore ducts.

## GREGARINA LAGENOÏDES (Léger) Labbé

[Figure 52]

1892	<i>Clepsidrina Lagenoïdes</i>	Léger	1892: 118
1899	<i>Gregarina lagenoides</i>	Labbé	1899: 11
1903	<i>Gregarina lagenoides</i>	Minchin	1903: 335
1911	<i>Gregarina lagenoides</i>	Wellmer	1911: 117

Sporonts in pairs, elongate. Length  $150\mu$ , width not given. Ratio LP : TL :: 1 : 3.5. WP : WD :: 1 : 1.3. Protomerite of primate cylindrical, with conical apex, the conical portion nearly equalling the cylindrical in length. Slight constriction at septum. Deutomerite constricted at end of anterior third, rapidly swelling to an almost perfect globe in posterior two-thirds. Satellite of practically same shape but less accentuated. Epimerite a simple spherical or ovoidal papilla.

Cysts spherical, dehiscing by spore-ducts, spores in chains. Spores biconical, blunt at poles.

Intestine of *Lepisma saccharina* L.

Taken in the Valley of the Creuse, France, and in East Prussia.

#### Species of Doubtful Position

#### ? GREGARINA PODURAE (Léger) Labbé

[Figures 53 and 54]

1892	<i>Clepsidrina Podurae</i>	Léger	1892: 119
1899	<i>Gregarina podurae</i>	Labbé	1899: 12
1903	<i>Gregarina podurae</i>	Minchin	1903: 336

Sporonts in pairs or threes. Maximum length  $90\mu$ . Protomerite either separated from deutomerite by septum or lacking the septum. Ratio LP : TL :: 1 : 5.5; WP : WD :: 1 : 1.8. In normal individuals protomerite dome-shaped, flattened apically. No constriction at septum. Deutomerite cylindrical, broadly truncate at base.

In individuals which lack the septum the whole animal is ovoidal with or without a very small papillate epimerite. Normal epimerite much larger, a slightly stalked papilla. The individuals which form associations of more than two are of the abnormal ovoidal type.

The protoplasm is gray-green with large orange granules. The nucleus is spherical, with one karyosome.

Cysts spherical,  $80\mu$ , one long spore-duct, spores in chains, 6.8 by  $3\mu$ .

Intestine of *Podura villosa* and *Orchesella* sp.

Taken in the Valley of the Loire, France.

This species seems to be an aberrant one representing a transitory species to another genus or an intestine in which for some reason the gregarines became abnormal. The possibility of more than one species being present is excluded from the same type of protoplasm of peculiar color and texture in both kinds of individuals. The author suggests that the species may be intermediate between the genus *Gamocystis*, in which a septum is always absent, and *Gregarina* in which it is always present.

*Gregarina* sp. Wellmer1911 *Gregarina* sp. Wellmer 1911: 146

There are no data whatever concerning this form.

Intestine of *Sminthurus fuscus* L.

Taken in East Prussia.

LIST OF SPECIES FOUND IN THE ORDER ISOPTERA OF  
THE CLASS HEXAPODA

## SPECIES OF DOUBTFUL POSITION

? *Gregarina termitis* Leidy*Termes flavipes*; *T. lucifugus* Rossi.

## Family GREGARINIDAE Labbé 1899: 9

Genus GREGARINA Dufour 1828: 366

? GREGARINA TERMITIS Leidy

[Figures 51 and 56]

1881	<i>Gregarina termitis</i>	Leidy	1881: 425
1897	<i>Gregarina termitis</i>	Porter	1897: 65
1899	<i>Gregarina termitis</i>	Labbé	1899: 36
1903	<i>Gregarina termitis</i>	Crawley	1903: 44
1903	" <i>Gregarina</i> " <i>termitis</i>	Minchin	1903: 337
1913	<i>Gregarina termitis</i>	Ellis	1913: 289

Sporonts solitary, obese ovoidal. Length  $60\mu$ , width  $36\mu$ . Ratio LP : TL :: 1 : 3.3 WP : WD :: 1 : 1.2. Protomerite dome-shaped, twice as wide as high, deep constriction at septum. Deutomerite ovoidal, tapering to a rather sharp point. Nucleus spherical, one karyosome.

Epimerite and cysts unknown.

Intestine of *Termes flavipes*; *T. lucifugus* Rossi.

Taken at Philadelphia, Pa., Cambridge, Mass., and Boulder, Colo.

Leidy found but one gregarine in his host, but Porter reports the parasites "very common in some hosts," in the anterior part of the small intestine only. Porter illustrates a section of the intestine in which are "great numbers of cysts." The sections, however, are undoubtedly those of adult sporonts cut crosswise and obliquely, with dark-staining nuclei often sectioned, as often not. A figure (Fig. 74, Pl. VI, of Porter) showing an adult solitary sporont in which the protoplasmic granules are fairly large and regularly spherical is described as "that of one filled with sporocysts." Porter's figure of a sporont is almost identical with that of Leidy (Plate 52, fig. 27).

Crawley opened "perhaps a dozen termites" in search for the parasite but did not encounter it.

I have examined many termites at different seasons. They were abundantly parasitised with Infusoria (Leidy 1881, and Kofoid and Swezey 1919) but no gregarines were recovered.

Ellis described the species from western termites. His drawing (my figure 56) compares favorably with that of Leidy except that the posterior end of his is broadly rounded instead of bluntly pointed. The newer specimens are also much larger— $570\mu$  long. Dimensions given by Ellis are "P.  $25\mu \times 170\mu$ , D.  $30\mu \times 400\mu$ ." They correspond with his figure (Pl. XVII, fig. 6) if changed to "P.  $250\mu$  by  $170\mu$ , D.  $300\mu$  by  $400\mu$ ."

This species is considered doubtful because three important characters are lacking, viz. epimerite, cyst and spores. None of the workers has encountered associations.

LIST OF SPECIES FOUND IN THE ORDER HEMIPTERA OF  
THE CLASS HEXAPODA

PARASITE	Host
ACTINOCEPHALIDAE	
<i>Coleorhynchus heros</i> (Schneider) Labbé	<i>Nepa cinerea</i> L.
UNCERTAIN SPECIES	
[? <i>reduvii</i> Ramdohr]	<i>Reduvius personatus</i> (L.)
MISCELLANEOUS	
[no name]	<i>Phymata crassipes</i>

Family ACTINOCEPHALIDAE Léger 1892: 166

Genus COLEORHYNCHUS Schneider 1885: 94, emend.  
Labbé 1899: 23

Epimerite unknown. Protomerite a rounded shallow disc depressed centrally with a cape overlapping the deutomerite. Septum convex upward. Simple rupture of cysts, spores biconical.

COLEORHYNCHUS HEROS (Schneider) Labbé Type Species

[Figures 48 and 49]

1885	<i>Coleophora heros</i>	Schneider	1885: 95
1899	<i>Coleorhynchus heros</i>	Labbé	1899: 23
1903	<i>Coleorhynchus heros</i>	Minchin	1903: 200, 335
1913	<i>Coleorhynchus heros</i>	Ellis	1913: 276

Sporonts solitary, length 2 to 3 mm. Width not given. Ratio LP : TL :: 1 : 4; WP : WD :: 1 : 1. Protomerite a round flattened disc centrally depressed, border slightly irregular with a cape extending down over the deutomerite. Septum convex upward. Deutomerite ovoidal, blunt at posterior end. Epimerite and nucleus not known.

Cyst dehiscence by simple rupture, spores sharply biconical.

Taken at Poitiers, France.

Intestine of *Nepa cinerea* L.



Uncertain Species  
[? *reduvii* Ramdohr]  
[Figure 50]

1811	<i>Vibrio Reduvii</i>	Ramdohr	1811: 194
1848	<i>Sporadina Reduvii</i>	Stein	1848: 213, 223
1848	<i>Sporadina Reduvii</i>	Frantzius	1848: 195
1859	<i>Gregarina Reduvii</i>	Diesing	1859: 734
1863	<i>Gregarina Reduvii</i>	Lankester	1863: 94
1899	<i>Hyalospora reduvii</i>	Labbé	1899: 14
1903	<i>Hyalospora reduvii</i>	Minchin	1903: 336

Taken at Berlin.

Intestine of *Reduvius personatus* (L.).

Ramdohr placed the species with the Infusoria, in the genus *Vibrio*.

Stein gives these dimensions:

Sie zeigten sehr verschiedene Grösse, die grössten waren etwa  $\frac{1}{5}$ ''' lang und  $\frac{1}{38}$ ''' breit

He also observed cysts in which two sporonts were united. Nine spore-ducts were seen, with spore extrusion in chains. The spores were

. . . kung spindelförmig oder fast eiförmig,  $\frac{1}{250}$ ''' by  $\frac{1}{570}$ '''.

His illustrations show them to be well-rounded at the ends.

The genus *Hyalospora*, in which the specimens recorded were placed by Labbé, is characterized in part by (a) sporonts in associations of two, (b) cysts with simple rupture, (c) spores fusiform, sharply pointed at the ends.

The species in question does not belong in this genus because (a) among the great numbers of parasites seen by Stein none is mentioned as found in association and his figure indicates a solitary individual, (b) cyst dehiscence is accomplished through spore-ducts (nine in the figure of Stein), and (c) with spores extruded in chains. The spores are ellipsoidal, rounded at the ends.

It is evident that the species belongs in the family Gregarinidae from the method of cyst dehiscence. I have placed it with the Uncertain Species because of insufficient data. It seems to most closely resemble the genus *Leidyana* Watson.

Miscellaneous

No Name

1828	<i>Gregarina Phymatae crassipedis</i>	Dufour	1828: 206
1837	<i>Gregarina soror</i>	Dufour	1837: 12
1846	<i>Gregarina soror</i>	Frantzius	1846: 11, 28
1851	<i>Gregarina soror</i>	Diesing	1851: 11
1863	<i>Gregarina soror</i>	Lankester	1863: 94
1903	<i>Gregarina soror</i>	Minchin	1903: 336

Dufour says concerning this animal life:

Subsphericum alba, cephalothorace abdominis dimidiam partem adaequante.

From the figure and description of Dufour it is obvious that what he observed were not sporonts but cysts. There is no record of sporonts being found, and the error was a very natural one at the time.

LIST OF SPECIES FOUND IN THE ORDER NEUROPTERA OF  
THE CLASS HEXAPODA

PARASITE	Host
<b>GREGARINIDAE</b>	
<i>Gregarina clavata</i> Kölliker	<i>Ephemera vulgata</i> larv.
<i>Gregarina mystacidarum</i> Frantzius	<i>Mystacides</i> sp., larv.
<i>Gregarina marteli</i> Léger	<i>Embia Solieri</i> Ramb., larv.
<i>Gamocys is ephemerae</i> (Frantzius) Labbé	<i>Ephemera vulgata</i> , larv.
	<i>Ephemera</i> sp., larv.
<b>ACTINOCEPHALIDAE</b>	
<i>Actinocephalus sieboldii</i> (Kölliker) Frantzius	<i>Agriion</i> sp., larv.
<i>Actinocephalus octacanthus</i> Frantzius	<i>Phryganea</i> sp.
<i>Actinocephalus brachydactylus</i> Ellis	<i>Aeschna</i> sp.
<i>Geneiorhynchus monnieri</i> Schneider	<i>Libellules</i> sp.
Type species	
<i>Genriorhynchus aeschnae</i> Crawley	<i>Aeschna constricta</i> Say.
<i>Bothriopsis claviformis</i> Pinto	<i>Aeschnida</i> sp., larv.
<i>Asterophora mucronata</i> Léger	<i>Rhyacophila</i> sp.
Type species	
<i>Asterophora elegans</i> Léger	<i>Phryganea grandis</i> , larv.
	<i>Sericostoma</i> sp., larv.
<i>Discorhynchus truncatus</i> (Léger) Labbé	<i>Sericostoma</i> sp. larv.
Type species	
<i>Pileocephalus chinensis</i> Schneider	<i>Mystacides</i> sp., larv.
Type species	
<i>Pileocephalus heerii</i> (Kölliker) Schneider	<i>Phryganea varia</i> (Fab.) larv.
<i>Hoplorhynchus oligacanthus</i> (von Siebold)	<i>Calopteryx virgo</i> L., larv.
Schneider	<i>C. splendens</i> Harb. larv.
Type species	
<b>ACANTHOSPORIDAE</b>	
<i>Ancyrophora uncinata</i> Léger	<i>Sericostoma</i> sp., larv.
	<i>Phryganea rhumbica</i> , larv.
	<i>Dytiscus</i> sp., larv.
	<i>Colymbetes</i> sp., larv.
	<i>Limnophilus rhombicus</i> , larv.
<i>Prismatospora evansi</i> Ellis	<i>Tramea lacerata</i> Hagen
Type species	<i>Sympetrum rubicundulum</i> Say
<b>MENOSPORIDAE</b>	
<i>Menospora polyacantha</i> Léger	Type species <i>Agriion puella</i> , larv.
<b>SPECIES OF DOUBTFUL POSITION</b>	
[? <i>psocorum</i> von Siebold]	<i>Psocus</i> sp.

## Family GREGARINIDAE Labbé 1899: 9

Genus GREGARINA Dufour 1828: 366

## GREGARINA CLAVATA Kölliker

[Figures 22 and 89]

1848	<i>Gregarina clavata</i>	Kölliker	1848: 10
1848	<i>Gregarina clavata</i>	Frantzius	1848: 194
1848	<i>Sporadina clavata</i>	Frantzius	1848: 195
1851	<i>Gregarina clavata</i>	Diesing	1851: 14
1859	<i>Gregarina clavata</i>	Diesing	1859: 734
1863	<i>Gregarina clavata</i>	Lankester	1863: 94
1863	<i>Zygocystis clavata</i>	Lankester	1863: 94
1887	<i>Clepsidrina granulosa</i>	Schneider	1887: 74, 77, 78
1899	<i>Gregarina granulosa</i>	Labbé	1899: 11
1903	<i>Gregarina granulosa</i>	Minchin	1903: 334
1911	<i>Gregarina granulosa</i>	Wellmer	1911: 119

Of the original observation by Kölliker only a single immature specimen is illustrated which furnishes a clue to the identity of the parasite. The sporont is short and stout, 30 by 16 $\mu$ , the ratio of LP : TL :: 1 : 2.5; WP : WD :: 1 : 1. The protomerite is dome-shaped with a small apical cone and a deep constriction at the septum. The deutomerite is ovoidal and the nucleus spherical with one karyosome.

Intestine of *Ephemera vulgata*, larva.

Taken at Zürich, Poitiers, France, and in East Prussia.

Kölliker records that Frantzius had found this species (1845) but Frantzius' drawings (1848, Pl. VII, figs. VII, 1, 2, 3, and 4) are very unlike the figure of Kölliker (Fig. 89, this paper) and represent clearly the species *Gamocystis ephemeræ*.

Diesing (1859) records:

Receptaculum subhemisphaericum apiculo terminali conico. Corpus longe ovatum, lacteum. Longit. 1/26''' ; crassit. 1/69'''.

Schneider (p. 74) reports finding *Gamocystis ephemeræ* and also another gregarine:

Le Grégarine qui domine qu'on trouve toujours dans ces larves, est la curieuse *Gamocystis Francisci*. Beaucoup plus rare et toujours en petit nombre est au contraire la Grégarine actuelle, qui se fait en revanche remarquer par une belle taille (518u le primitive).

It is characterized by the very large granules in the endocyte of the protomerite. Chromidial inclusions in the deutomerite. Ratio LP : TL :: 1 : 5 (Primitive) to 1 : 9 (Satellite). WP : WD :: 1 : 1.5. The nucleus is spherical, 51 $\mu$  in diameter with one karyosome 26 $\mu$  in diam. The sporont is cylindrical, the protomerite dome-shaped with a deep constriction at the septum. The deutomerite is cylindrical with a shoulder and truncate at the free end.

While the observations of the two authors are not comparable, the first from an immature specimen only, yet there is a probability of their being identical, the hosts being the same. In order therefore to reduce the number of older incompletely described species they should be absorbed wherever possible. In the present species there are at least no conflicting characters.

#### GREGARINA MYSTACIDARUM Frantzius

[Figure 76]

1848	<i>Gregarina Mystacidarum</i>	Frantzius	1848: 193, 196
1848	<i>Gregarina Mystacidarum</i>	Stein	1848: 188
1851	<i>Gregarina Mystacidarum</i>	Diesing	1851: 12
1859	<i>Gregarina Mystacidarum</i>	Diesing	1859: 734
1863	<i>Gregarina Mystacidarum</i>	Lankester	1863: 94
1875	<i>Clepsidrina mystacidarum</i>	Schneider	1875: 592
1899	<i>Gregarina mystacidarum</i>	Labbé	1899: 11
1903	<i>Gregarina mystacidarum</i>	Minchin	1903: 335
1911	<i>Gregarina mystacidarum</i>	Wellmer	1911: 118

Sporonts in pairs, long-cylindrical, Ratio LP:TL::1:6 to 10; WP:WD::1:1. Protomerite cylindrical, truncate at free end, slightly constricted at septum. Deutomerite cylindrical, broadly rounded posteriorly. Nucleus spherical. Epimerite not known. Cysts spherical.

Taken at Berlin and in East Prussia. Host *Mystacides* sp., larva.

This host is also parasitized by *Pileopcehalus chinensis* Schn.

#### GREGARINA MARTELI Léger

[Figures 36 and 37]

1904	<i>Gregarina Marteli</i>	Léger	1904: 358
1911	<i>Gregarina Marteli</i>	Sokolow	1911: 279

Sporonts in pairs, elongate, slender. Length 100 to 150 $\mu$ . Width not given. Ratio LP:TL::1:10; WP:WD::1:1. Protomerite of primate conoidal, blunt at apex and dilated in posterior two-thirds. Protomerite, of satellite deeply cupped in anterior portion. Constriction at septum. Deutomerite elongate-cylindrical, of same width throughout, ending in a broad blunt extremity. Epimerite a simple globular papilla. Nucleus spherical. Cyst and spores unknown.

Host: *Embia Solieri* Ramb., larv. Intestine.

Taken at Cavaliere, France.

This host is also parasitized with *Diplocystis clerici* Léger (Monocystid Gregarine) and *Adela transita* Léger (Coccidian).

Genus GAMOCYSTIS Schneider 1875: 586; 1882: 443

Sporonts biassociative, united in apposition, ovoidal, stout-bodied, resembling a Monocystid. Protomerite only in trophozoite. Sporulation partial. Cyst without spore-ducts. Spores elongate-cylindrical.



## GAMOCYSTIS EPHEMERAE (Frantzius) Labbé

[Figures 38 and 90]

1843	<i>Zygocystis Ephemeræ</i>	Frantzius	1843: 194
1848	<i>Gregarina clavata</i>	Kölliker	1848: 10
1848	<i>Zygocystis Ephemeræ</i>	Frantzius	1848: 194
1851	<i>Gregarina clavata</i>	Diesing	1851: 553
1859	<i>Gregarina Ephemeræ</i>	Diesing	1859: 736
1882	<i>Gamocystis Francisci</i>	Schneider	1882: 444
1887	<i>Gamocystis Francisci</i>	Schneider	1887: 74
1899	<i>Gamocystis ephemeræ</i>	Labbé	1899: 12
1903	<i>Gamocystis ephemeræ</i>	Minchin	1903: 197, 334

Sporonts in pairs, in apposition. No protomerite. Body broadly ovoidal, truncate at apices, flattened at place of union. Length of primate  $110\mu$ , of satellite  $130\mu$ . Width of former  $80\mu$ , of latter same. Sarcocyte thickened at the two apices. Endocyte dense, with large irregular granules. Nucleus spherical,  $30\mu$ , one karyosome. Cyst and spores not known.

Intestine of *Ephemeræ* sp., larva, *Ephemeræ vulgata*, larva.

Taken at Zürich and in Indre-et-Loire, France.

There seems to be no doubt that the species seen by Frantzius and by Schneider are identical from a comparison of the figures given by each. The ratio of length to width in the figures of Frantzius is about two to one, in the figure of Schneider one and one-half to one.

Labbé considers Kölliker's *Gregarina clavata* identical with the above species, probably because of a similarity of the host. The species are, however, quite different.

Minchin considers the present species identical with *Gamocystis francisci* Schn.

Schneider (1882: 445) offers this phylogenetic hypothesis: The genus *Ephemeræ* has been considered a pseudo-neuropteran closely allied to the Orthoptera, in which group the only other species of the genus *Gamocystis* has been found.

Family ACTINOCEPHALIDAE Léger 1892: 166

Genus ACTINOCEPHALUS Stein 1848: 196

Epimerite small, sessile or upon a short neck, with 8 to 10 short sharp spines or simple bifurcate digitiform processes. Spores biconical.

## ACTINOCEPHALUS SIEBOLDII (Kölliker) Frantzius

[Figure 12]

1839	?	von Siebold	1839: 67
1848	<i>Gregarina Sieboldii</i>	Kölliker	1848: 10
1848	<i>Actinocephalus Sieboldii</i>	Frantzius	1848: 195
1851	<i>Gregarina Sieboldii</i>	Diesing	1851: 7
1859	<i>Gregarina Sieboldii</i>	Diesing	1859: 731
1863	<i>Gregarina oligacantha</i>	Lankester	1863: 94
1899	<i>Hoplorhynchus oligacanthus</i>	Labbé	1899: 30

Sporonts solitary, rather obese. Total length '0.162 to 0.188''' (Kölliker), Width 0.045''' . Ratio LP : TL :: 1 : 4 to 5; WP : WD :: 1.3 : 1. Protomerite rounded, slightly wider than high, constriction at septum. Deutomerite narrower than protomerite, tapering to a blunt posterior extremity. Epimerite composed of 4 to 6 sharp recurved hooks set upon a long cylindrical neck. Nucleus spherical with one or two large karyosomes.

Host: Larva of several species of Agrion. Intestine.

Taken at Danzig, Wurtzburg.

Kölliker says this species was first taken by von Siebold but not described. Kölliker described it in detail and assigned to it a name.

Frantzius placed it in the genus *Actinocephalus* because of the character of the epimerite.

Labbé placed the species with *Hoplorhynchus oligacanthus* Schn. because of a close similarity with this genus. While the epimerites of the two species are similar, Kölliker's species having 4 to 6 recurved hooks and Schneider's 6 to 8, the hooks on the former species are sharply pointed and decidedly recurved while those on the latter number eight as a maximum and are but slightly recurved and blunt at the tips. (Cf. Figs. 13 and 14 (*Hoplorhynchus oligacanthus*) with Fig. 12, the present species).

The writer has differentiated the two species on this point and a dissimilarity of the nuclei. Schneider's new genus, *Hoplorhynchus*, is characterized by an elongate-ovoidal nucleus while the nucleus in Kölliker's species is spherical.

#### ACTINOCEPHALUS OCTACANTHUS Frantzius

[Figure 74]

1848	<i>Gregarina Heerii</i>	Frantzius	1848: 193
1848	<i>Actinocephalus octacanthus</i>	Frantzius	1848: 192, 194, 195
1851	<i>Gregarina Heerii</i>	Diesing	1851: 552
1851	<i>Gregarina Frantziusiana</i>	Diesing	1851: 8
1863	<i>Gregarina Heerii</i>	Lankester	1863: 94

Host: *Phryganea* sp. Intestine.

Frantzius recognized that this species was different from the *Gregarina Heerii* of Kölliker from the same host, and illustrates epimerites of the two species, but his drawings are confusing for in another place he calls the same drawing now one name, now the other.

Diesing regarded the two species as synonymous on one page (552) and still separates them on another, creating a new species for the present species, *Gregarina frantziusiana*. He differentiates the two thus:

*Gregarina frantziusiana* Diesing:

Proboscis globosa, uncinulorum, octo coronula terminali simplici (octolobia Frantzius).  
 Corpus subellipticum turgidum . . . .

*Gregarina heerii* K  lliker.

Proboscis antrorsum obovato-lanceolata, granulis exasperata, retrorsum subelliptica laevis, inermis? . . . . Corpus longe ovatum . . . .

Hab. *Phryganea grandis* larva, intestine, in both.

From then on the present species is lost in the species *Pileocephalus heerii*. It is obvious from a comparison of the epimerites that two very different species have been confused and that the original designation of Frantzius still holds.

## ACTINOCEPHALUS BRACHYDACTYLUS Ellis

[Figures 44 and 45]

1913 *Actinocephalus brachydactylus* Ellis 1913: 279, 289

Sporonts solitary, elongate-ovoidal. Length 501 $\mu$ . Ratio LP: :1:3 to 4; WP:WD: :1:1. Protomerite well-rounded, with same width as height, slight constriction at septum. Deutomerite slightly wider at shoulder, tapering gently and ending in a blunt point. Epimerite very short, a corona of eight short digitiform processes.

Cyst and spores unknown.

Habitat not given. Host: Nymphs of *Aeschna* sp.

Taken at Douglas Lake, Michigan.

Genus GENEIORHYNCHUS Schneider 1875: 594

Epimerite a tuft of short bristles set at the apex of a long slender neck. Spores cylindro-biconical.

GENRIORHYNCHUS MONNIERI Schneider Type species

[Figures 19, 20, and 21]

1875 *Geneiorhynchus Monnieri* Schneider 1875: 595

1899 *Geneiorhynchus monnieri* Labb   1899: 25

1903 *Geneiorhynchus monnieri* Minchin 1903: 200, 335

1913 *Geneiorhynchus monnieri* Ellis 1913: 274

Sporonts solitary, obese, ovoidal. No dimensions given. Ratio LP:TL: :1:4; WP:WD: :1:1.3. Protomerite very broadly rounded, acuminate at apex. Slight constriction at septum. Deutomerite widest at mid-portion, ending in an acute point. Epimerite a tuft of short sharp bristles set at apex of a long slender neck. Nucleus spherical with several karyosomes. Cyst dehiscence by simple rupture, spores sub-navicular.

Intestine of *Libellules* sp.

Taken near Paris.

## GENEIORHYNCHUS AESCHNAE Crawley

[Figure 40]

1907	<i>Geneiorhynchus aeshnae</i>	Crawley	1907: 227
1911	<i>Geneiorhynchus aeshnae</i>	Sokolow	1911: 282
1913	<i>Generorhynchus aeshnae</i>	Ellis	1913: 275, 289

Sporonts solitary, cylindrical. Length of trophozoite  $420\mu$ . Ratio (without epimerite) LP:TL: :1:3. WP:WD: :1.1:1 Protomerite widest at base, curving gently anteriorly, ending in a truncate cone. No constriction at septum. Deutomerite narrower than protomerite at septum, tapering thence and ending in a broad truncated extremity. Epimerite a large globular papilla borne on a short stout neck from the protomerite and "liberally provided with short spines directed backward." (Crawley). Nucleus spherical with several karyosomes. Sarcocyte in apex of protomerite very thick. Endocyte not dense, nucleus visible in vivo. Cyst and spores not known.

Intestine? of *Aeschna coustricta* Say. (*Aeschna c.*)

Taken in Southeastern Pennsylvania.

Genus BOTHRIOPSIS Schneider 1875: 596

Epimerite an ovoidal structure with six or more long slender filaments. Protomerite very large, septum convex upward. Spores biconical.

## BOTHRIOPSIS CLAVIFORMIS Pinto

[Figure 61]

1918	<i>Bothriopsis claviformis</i>	Pinto	1918: ?
1919	<i>Bothriopsis claviformis</i>	Pinto	1919: 87

Sporonts elongate-triangular, widest at anterior end, bluntly acuminate posteriorly. Dimensions: 100 to  $200\mu$  in length, 70 in width (of protomerite). Ratio LP:TL: :1:7; WP:WD: :1.4 : 1. Nucleus spherical to irregular in shape.

Intestine of *Aeschnida* sp.

Taken at Manguinhos, Brazil.

Genus ASTEROPHORA Léger 1892: 129

Epimerite a thick long disc with a milled border and a long stout style projecting upward from the center. Spores cylindro-conical.

## ASTEROPHORA MUCRONATA Léger Type species

[Figures 25 and 26]

1892	<i>Asterophora mucronata</i>	Léger	1892: 130
1899	<i>Asterophora mucronata</i>	Labbé	1899: 22
1903	<i>Asterophora mucronata</i>	Minchin	1903: 200, 336

Sporonts solitary, elongate-ovoidal. Length  $350\mu$ , width not given. Ratio LP:TL: :1:2.2. WP:WD: :1:1.1. Protomerite elongate (twice as



long as wide), tapering upward from septum to a blunt conoidal anterior end. Deep constriction at septum. Deutomerite of same shape as protomerite and but little longer. Epimerite a flat disc with milled border and long blunt central style set upon a fairly stout neck. Nucleus ovoidal with several karyosomes. Cysts spherical, 150–200 $\mu$ . Dehiscence by simple rupture. Spores cylindro-biconical, 8 by 3.5 $\mu$ .

Host: Larva of *Rhyacophila* sp. Intestine.

Taken in the Valley of the Loire, France.

### ASTEROPHORA ELEGANS Léger

[Figures 23, 24, and 43]

1892	<i>Asterophora elegans</i>	Léger	1892: 131
1899	<i>Asterophora elegans</i>	Labbé	1899: 22
1903	<i>Asterophora elegans</i>	Minchin	1903: 200, 336

Sporonts solitary, elongate ovoidal. Length 450 $\mu$ . Width not given. Ratio LP:TL: :1:3; WP:WD: :1:1.1. Protomerite very elongate (almost twice as long as wide), tapering regularly upward from septum to a long blunt anterior end. Deep constriction at septum. Deutomerite of same shape as protomerite but twice as long. Epimerite a flat disc with a milled border and a short central style set upon a fairly stout neck which is of the same length as the protomerite. Nucleus slightly ovoidal with several karyosomes.

Cysts spherical, 300 to 400 $\mu$ . Spores biconical, much larger than in *Asterophora mucronata*, 12.7 by 4.25 $\mu$ .

Intestine of *Phryganea grandis*, larva, *Sericostoma* sp., larva.

The former host is also parasitized with *Pileocephalus heerii*, the two parasites generally found together. *Sericostoma* is also parasitized with *Discorhynchus truncatus*.

Genus DISCORHYNCHUS Léger 1892: 134; Labbé 1899: 20

Epimerite a short-stalked, large flattened globular structure with a still larger horizontal collar around its base. Spores biconical.

### DISCORHYNCHUS TRUNCATUS (Léger) Labbé Type species

[Figures 28 and 29]

1892	<i>Discorhynchus truncatus</i>	Léger	1892: 134
1899	<i>Discorhynchus truncatus</i>	Labbé	1899: 20
1903	<i>Discorhynchus truncatus</i>	Minchin	1903: 199, 337
1913	<i>Discorhynchus truncatus</i>	Ellis	1913: 275

Sporonts solitary, almost rectangular. Length  $300\mu$ , width not given. Ratio LP:TL: :1:4; WP:WD: :1.2 : 1. Protomerite irregularly rounded, bluntly conoidal at apex, widest at mid-portion. Constriction at septum. Protomerite wider than deutomerite. Deutomerite rectangular, in optical section, flat at base. Epimerite a short stout neck with a large flattened papilla at apex. Around the base of the papilla fits a much larger flattened disc like a collar. Nucleus spherical, with several karyosomes.

Cysts spherical,  $140\mu$ . Spores biconical, slightly crescentic.

Taken in Poitou, France.

Intestine of a neuropteran doubtfully identified as the larva of *Sericoctoma* sp.

#### Genus PILEOCEPHALUS Schneider 1875:591

Epimerite a small lance-shaped or simple conoidal papilla placed unstalked upon the protomerite. Spores biconical.

#### PILEOCEPHALUS CHINENSIS Schneider Type species

[Figures 17, 18, 93, and 94]

1875	<i>Pileocephalus chinensis</i>	Schneider	1875: 592
1885	<i>Pileocephalus chinensis</i>	Schneider	1885: 10
1899	<i>Pileocephalus chinensis</i>	Labbé	1899: 19
1903	<i>Pileocephalus chinensis</i>	Minchin	1903: 199, 335
1911	<i>Pileocephalus chinensis</i>	Wellmer	1911: 128
1913	<i>Pileocephalus chinensis</i>	Ellis	1913: 274

Sporonts solitary, stout bodied, ovoidal. Measurements not given; “. . . toujours de taille assez petite . . .” Ratio LP:TL: :1:5; WP:WD: :1:1. Protomerite broadly rounded, apex pointed, slightly wider than high. Constriction at septum. Deutomerite widest at shoulder, tapering from thence and ending in a broad blunt extremity. Epimerite a small unstalked papilla, conoidal at apex. Nucleus spherical.

Cysts spherical, spores roughly triangular with long slender ends. (Figs. 93, 94.)

Taken near Paris.

Intestine of *Mystacides* sp., larva.

This species received its name from the character of the epimerite concerning which Schneider says:

Epimérite triangulaire ou cordiforme en manière de bonnet chinois . . .

The insect is also the host of *Gregarina mystacidarum* Frantzius, and Schneider and Wellmer found associations of the parasite in the host with the above described species.

## PILEOCEPHALUS HEERII (Kölliker) Schneider

[Figures 15, 16, 46, 72 and 73]

1845	<i>Gregarina Heerii</i>	Kölliker	1845: 100
1848	<i>Gregarina Heerii</i>	Kölliker	1848: 6
1848	<i>Gregarina Heerii</i>	Frantzius	1848: 193
1848	<i>Stylorhynchus Heerii</i>	Frantzius	1848: 195
1851	<i>Gregarina Heerii</i>	Diesing	1851: 552
1851	<i>Gregarina Frantziusiana</i>	Diesing	1851: 8
1859	<i>Gregarina Heerii</i>	Diesing	1859: 728
1859	<i>Gregarina Frantziusiana</i>	Diesing	1859: 730
1863	<i>Stylorhynchus Heerii</i>	Carus	1863: 570
1863	<i>Gregarina Heerii</i>	Lankester	1863: 95
1887	<i>Pileocephalus Heerii</i>	Schneider	1887: 199
1899	<i>Pileocephalus heerii</i>	Labbé	1899: 19
1903	<i>Pileocephalus heerii</i>	Minchin	1903: 199, 336

Sporonts solitary, capable of great contractility due to unusually well-developed myonemes. Trophozoite when quiescent long and arrow-shaped, widest in middle and tapering in both directions, sharply acuminate at extremities (Fig. 15). In sporonts the same general shape but much contracted longitudinally and proportionally broader. (Fig. 16). Dimensions not given. Ratio LP:TL: : (quiet trophozoite without epimerite) 1:3 (contracted sporont 1:2). WP:WD: :1:1. Protomerite widest just above septum, conical, apex truncate. Deep constriction at septum. Deutomerite same shape, ending acuminately. Nucleus ellipsoidal with many small karyosomes. Epimerite highly specialized. In young trophozoites an elongate papilla sharply acuminate and situated upon a short neck. In older specimens there develops a spade-shaped or lanceolate (in optical section) holdfast, at the end of a bulbous neck (the former papilla). The neck and lance are of equal length and surmount the truncate protomerite. The trophozoite in this form is a very beautiful animal (Fig. 15).

Spores from cysts in feces biconical, which is the accepted form for the type, as mentioned in the genus synopsis.

A possible schizogony exists, for in this species cysts were encountered in the coelom which developed triangular spores. Schneider attributes these latter spores to the species in question but he suggests that they may belong to another parasite. If the discovery is authentic, the fact adds one link in the hypothesis of Minchin that the Cephaline Gregarines are capable of schizogony as well as sporogony. If this should be proven an impossibility, then the present species must be removed from the Eugregarinae and placed with the Schizogregarinae.

Schneider found only triangular spores in the type species *P. chinensis*, but does not state whether they emanated from coelomic or fecal cysts, mentioning only the latter type of cysts.



Habitat: Intestine of *Phryganea varia* (Fabricius), larva.

Taken at Wurzburg, and Poitiers (France).

Kölliker gives as hosts *Phryganea grandis* 'and other Phryganeidae larvae.' The only point of serious conflict between the two sets of observations lies in the shape of the nucleus. We are led to believe this one of the fixed characters of a species, but Kölliker finds the nucleus to be spherical, while Schneider says it is ovoidal. In *P. chinensis*, however, it is spherical, so this is not a genus character.

Schneider does not doubt the identity of the two species.

La figure donnée par Kölliker ne laisse aucun doute sur la synonymie, . . .

Frantzius gives a beautiful figure of a trophozoite which agrees in every particular with the observations of others except that the nucleus here too is spherical (Fig. 72, this paper). I am inclined to think Schneider's observations were in error or mis-interpreted in the rapidly moving animals and that the correct shape in all three sets of data is spherical.

#### Genus HOPLORHYNCHUS Carus 1863:570

Sporonts slender with elongate ovoidal nuclei. Epimerite a very long neck with six to eight slightly recurved hooks. Cyst dehiscence by simple rupture. Spores ellipsoidal.

#### HOPLORHYNCHUS OLIGACANTHUS (von Siebold) Schneider

Type species  
[Figures 13 and 14]

1839	<i>Gregarina oligacanthus</i>	von Siebold	1839: 67
1845	<i>Gregarina oligacantha</i>	Dujardin	1845: 638
1845	<i>Gregarina oligacantha</i>	Kölliker	1845: ?
1848	<i>Gregarina oligacantha</i>	Kölliker	1848: 10
1848	<i>Stylorhynchus oligacanthus</i>	Stein	1848: 195, 222
1848	<i>Stylorhynchus oligacanthus</i>	Frantzius	1848: 195
1851	<i>Gregarina oligacantha</i>	Diesing	1851: 7
1859	<i>Gregarina oligacantha</i>	Diesing	1859: 730-1
1863	<i>Gregarina oligacantha</i>	Lankester	1863: 95
1875	<i>Hoplorhynchus oligacanthus</i>	Schneider	1875: 591
1899	<i>Hoplorhynchus oligacanthus</i>	Labbé	1899: 30
1903	<i>Hoplorhynchus oligacanthus</i>	Minchin	1903: 201, 333
1911	<i>Hoplorhynchus oligacanthus</i>	Wellmer	1911: 139
1913	<i>Hoplorhynchus oligacanthus</i>	Ellis	1913: 275

Sporonts solitary, slender. Dimensions not given. Ratio LP:TL: : 1:4; WP:WD: :1:1. Protomerite irregularly rounded, slightly wider than deutomerite. Widest at mid-region, constricted at septum. Deutomerite irregularly cylindrical, tapering posteriorly and ending in a blunt point. Epimerite a corona of six to eight slightly recurved hooks set upon a long



slender cylindrical neck. Nucleus elongate-cylindrical with many small karyosomes.

Cyst and spores as in genus characters.

Intestine of *Calopteryx* (*Callopteryx*, Schneider) *virgo* L., larva, and *C. splendens* Harb. larva.

Taken at Danzig, Berlin and Paris.

With all the authors who mention the species, only one gives adequate figures, Schneider, from whom the data and drawings is taken.

Diesing (1859) reports:

Proboscis longissima gracilis medio ventricosa, apice subglobosa, spinularum (circa 9) corona simplici. Receptaculum subglobosum compressum. Corpus conicum lacteum receptaculo quinque longius.

Lankester considers *Actinocephalus sieboldii* and the present species synonymous.

#### Family ACANTHOSPORIDAE, Léger 1892: 167

Sporonts solitary, epimerite simple or appendicular. Dehiscence by simple rupture. Spores with equatorial and polar spines.

#### Genus ANCYROPHORA Léger 1892: 146

Epimerite a globe with a corona of not more than 12 backwardly-directed blunt hooks. Spores biconical with equatorial and polar spines.

#### ANCYROPHORA UNCINATA Léger

[Figures 27, 41 and 42]

1848	<i>Gregarina Dytiscorum</i>	Frantzius	1848: 194
1892	<i>Ancyrophora uncinata</i>	Léger	1892: 147
1899	<i>Ancyrophora uncinata</i>	Labbé	1899: 28
1903	<i>Ancyrophora uncinata</i>	Minchin	1903: 201, 335
1916	<i>Ancyrophora uncinata</i>	Watson	1916a: 164

Sporonts solitary, elongate. Length 150–200 $\mu$ . Protomerite well rounded, deeply constricted at septum. Deutomerite widest at shoulder, tapering from thence to a long slender acuminate posterior extremity. Epimerite a corona of twelve or less short blunt recurved hooks, superimposed upon a distinct but rather short stout neck. The hooks are arranged in two levels, the upper group being larger and stouter. Nucleus spherical with several karyosomes.

Cysts spherical, 200 $\mu$ , spores biconical, hexagonal in optical section, with four spines at each pole and six on equator. Spores 8 by 6 $\mu$ .

Intestine of larvae of *Sericostoma* sp., *Phryganea rhumbica*, and of two beetles, *Dytiscus* sp. and *Colymbetes* sp. Minchin adds *Limnophilus rhombicus*, probably a synonym of the second.

Taken in France.

The fact that this species is found in such widely varying hosts is unusual but not unique in the history of gregarines.

Genus PRISMATOSPORA Ellis 1914: 215

Spores hexagonal, truncate at ends with one row of long spines at each pole. Epimerite subglobose with lateral recurved hooks.

PRISMATOSPORA EVANSI Ellis Type species

[Figures 95, 96, 97, and 99]

1914 *Prismatospora evansi* Ellis 1914: 215

Sporonts broadly conical  $400\mu$  in average length. Ratio LP:TL: : 1:3; WP:WD: : 1:1. Protomerite broad, blunt, deutomerite tapering. Nucleus small, spherical.

Cysts subspherical,  $370\mu$  in diameter. Dehiscence by simple rupture. Spores as in genus, six long spines encircling each pole a short distance from the end, 11 by  $5.8\mu$ .

Intestine of *Tramea lacerata* Hagen. and *Sympetrum rubicundulum* Say.

Taken at Douglas Lake, Michigan.

The sporonts of this species are peculiar in that the protomerite is drawn out into digitiform processes at the apex in vivo, which may aid the animal in retaining its hold upon the intestine in so active a host where abdominal contractions might thrust it from the canal. These processes disappear when the animal is placed in water.

Family MENOSPORIDAE Léger 1892:168

Sporonts solitary. Epimerite a large cup bordered with hooks and placed on a long slender collar. Cyst dehiscence by simple rupture. Spores crescentic, smooth.

Genus MENOSPORA Léger 1892:151, 168

Characters of the family.

MENOSPORA POLYACANTHA Léger Type species

[Figures 30, 31 and 32]

1892	<i>Menospora polyacantha</i>	Léger	1892: 151
1899	<i>Menospora polyacantha</i>	Labbé	1899: 30
1903	<i>Menospora polyacantha</i>	Minchin	1903: 201, 332
1913	<i>Menospora polyacantha</i>	Ellis	1913: 275

Sporonts ovoidal, lanceolate,  $600-700\mu$  in length. Width not given. Ratio LP:TL: : (trophozoite, without epimerite) 1:5; WP:WD: : 1:1.1. Protomerite well rounded, deeply constricted at septum. Deutomerite widest just below septum, tapering gradually to a long sharply pointed

extremity. Epimerite a deep urn bordered with many short recurved hooks, superimposed upon a long slender neck two-thirds as long as the whole animal. Nucleus elongate-ovoidal, with one dumb-bell shaped karyosome.

Cysts spherical,  $200\mu$ , spores smooth crescents 15 by  $4\mu$ .

Taken in Poitou, France.

Intestine of *Agrion puella*, larva.

#### Species of Uncertain Position

[? psocorum von Siebold]

1839	<i>Gregarina Psocorum</i>	von Siebold	1839: 67
1846	<i>Gregarina Psocorum</i>	Frantzius	1846: 25
1848	<i>Gregarina Psocorum</i>	Frantzius	1848: 195
1851	<i>Gregarina ovata</i>	Diesing	1851: 10
1863	<i>Gregarina Psocorum</i>	Lankester	1863: 94
1911	<i>Hyalospora psocorum</i>	Wellmer	1911: 124

The only data outside the original reference, which is not available, are those of Diesing (1851):

Proboscis . . . . Receptaculum compressum. Corpus ovalum utrinque obtusum, receptaculo triplo longius. Longit. crassit . . .

Host: *Psocus* sp.

#### LIST OF SPECIES FOUND IN THE ORDER LEPIDOPTERA OF THE CLASS HEXAPODA

PARASITE	Host
GREGARINIDAE	
<i>Leidyana tinei</i> Keilin	<i>Endrosis fenestrella</i> Stain., larv.
UNNAMED SPECIES Keilin	<i>Oecophora pseudopretella</i> Stain., larv.
	<i>Tinea pallescentella</i> Stain., larv.

Family GREGARINIDAE Labbé 1899: 9

Genus LEIDYANA Watson 1915: 35

Sporonts solitary, epimerite a small sessile knob, dehiscence by spore-ducts. Spores in chains, barrel-shaped.

#### LEIDYANA TINEI Keilin

[Figures 115 and 116]

1918	<i>Leidyana tinei</i>	Keilin	1918: 406
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Sporonts solitary, long-ellipsoidal. Ratio LP:TL: :1:7.5; WP:WD: :1:1.7. Maximum length  $300\mu$ , width  $85\mu$ . Protomerite hemispherical, deutomerite regularly ellipsoidal, tapering gently to a blunt posterior end.

Cysts spherical  $110\mu$  in diameter. Spores barrel-shaped,  $7\mu$  long.

Intestine of *Endrosis fenestrella* Stain.

Taken at Cambridge, England.

### Unnamed Species Keilin

1918 Unnamed species Keilin 1918: 406

Intestine of *Oecophora pseudospretella* Stain, and *Tinea pallescentella* Stain.

Taken at Cambridge, England.

"Very similar to species here described," above, but a complete life-cycle was not procured, and the specimens left unnamed.

### LIST OF SPECIES FOUND IN THE ORDER DIPTERA OF THE CLASS HEXAPODA

PARASITE	HOST
<b>GREGARINIDAE</b>	
<i>Gregarina longa</i> (Léger) Labbé	<i>Tipula</i> sp., larva
<i>Gregarina ctenocephalus</i> Ross	<i>Ctenocephalus serraticeps</i>
<i>Hirmocystis ventricosa</i> (Léger) Labbé	<i>Tipula oleracea</i> , larv.
Type species	
<i>Hirmocystis polymorpha</i> (Léger) Labbé	<i>Limnobia</i> sp., larv
	<i>Systenocerus caraboides</i> L., larv.
<b>ACTINOCEPHALIDAE</b>	
<i>Actinocephalus tipulae</i> (Hammerschmidt)	<i>Tipula oleracea</i> L., larv.
Léger	<i>Pachyrhina pratensis</i> L., larv.
<i>Actinocephalus</i> sp. Léger	<i>Ctenophora</i> sp., larv.
<i>Schneideria caudata</i> (von Siebold) Léger	<i>Sciara nitidicollis</i> Meig. larv.
<i>Schneideria mucronata</i> Léger Type species	<i>Bibio marci</i> (L.), larv.
<i>Schneideria</i> sp.	<i>Chironomus</i> sp., larv.
<i>Stylocystis praecox</i> Léger Type species	<i>Tanytus</i> sp., larv.
<i>Taeniocystis mira</i> Léger Type species	<i>Ceratopogon solstitialis</i> Winn., larv.
<i>Pileocephalus striatus</i> Léger and Duboscq	<i>Ptychopiera contaminata</i> , larv.

### Family GREGARINIDAE Labbé 1899: 9

#### Genus GREGARINA Dufour 1828

#### GREGARINA LONGA (Léger) Labbé

[Figure 7]

1892	<i>Clepsidrina longa</i>	Léger	1892: 117
1899	<i>Gregarina longa</i>	Labbé	1899: 11
1903	<i>Gregarina longa</i>	Minchin	1903: 337
1911	<i>Gregarina longa</i>	Wellmer	1911: 114

Sporonts in pairs, very slender and elongate. Maximum length of sporont 500 $\mu$ . Width not given. Ratio LP:TL: :1: 10 to 12; WP:WD: : 1:1.2. Another form is found in which this ratio exists: LP:TL: :1:7, body less slender. Protomerite of primate well-rounded, deeply constricted at septum. Protomerite of satellite flattened at top, constricted in middle. Deutomerite regularly cylindrical, of approximately same width throughout in primate and tapering very slightly in satellite, ending in a broad blunt extremity. Epimerite a simple spherical papilla. Nucleus large, spherical, with one large karyosome.



Cysts spherical, 140 $\mu$ . Dehiscence by 7 or 8 short spore-ducts. Spores extruded in chains, dolioform, 6 by 5 $\mu$ .

Intestine of *Tipula* sp., larva.

Taken in the Valleys of the Vienne and Loire, France and in East Prussia.

#### GREGARINA CTENOCEPHALUS Ross

1909 *Gregarina ctenocephalus canis* Ross 1909: 359

1922 *Gregarina ctenocephalus* Kamm 1922 (this paper)

Sporonts spherical, no dimensions given. Epimerite pyriform, spores barrel-shaped. No dimensions given.

Intestine of *Ctenocephalus serraticeps*.

Taken at Port Said, Egypt.

Genus *HIRMOCYSTIS* Léger 1892: 110, emend. Labbé 1899: 12

Associations of from two to twelve sporonts. Epimerite small, cylindrical papilla. Cyst dehiscence by simple rupture. Spores ovoidal.

#### HIRMOCYSTIS VENTRICOSA (Léger) Labbé Type species

[Figures 8 and 9]

1892 *Eirmocystis ventricosa* Léger 1892: 111

1899 *Hirmocystis ventricosa* Labbé 1899: 13

1900 *Eirmocystis ventricosa* Magalhães 1900: 39

1903 *Eirmocystis ventricosa* Minchin 1903: 336, 337

1911 *Hirmocystis ventricosa* Wellmer 1911: 123

1913 *Eirmocystis ventricosa* Ellis 1913: 264

Sporonts bi- or rarely tri- associative, obese. Length 180 $\mu$ , width not given. Ratio LP:TL: :1:3.5. WP:WD: :1:1.5 Protomerite broadly rounded in front, widest in the anterior half, much constricted and cylindrical in second half. No constriction at septum. Deutomerite broadens appreciably just below septum, widest in anterior third, tapering from thence, ending in a square extremity. Epimerite a small cylindro-conical papilla. Nucleus spherical, one karyosome.

Cysts spherical, 100 $\mu$ , dehiscence by simple rupture, spores ovoidal, not fusiform, 9 $\mu$  by 6 $\mu$ .

Intestine of *Tipula oleracea* and *Pachyrhina pratensis*, larvae.

Taken in the Valley of the Loire, France and in East Prussia.

*Tipula* sp. is also parasitized by *Gregarina longa* and *Actinocephalus tipulae*.

#### HIRMOCYSTIS POLYMORPHA (Léger) Labbé

[Figures 10 and 11]

1892 *Eirmocystis polymorpha* Léger 1892: 113

1899 *Hirmocystis polymorpha* Labbé 1899: 13

1903 *Eirmocystis polymorpha* Minchin 1903: 197, 335

1911 *Hirmocystis polymorpha* Wellmer 1911: 123

Sporonts in associations of from two to twelve, arranged linearly or bi- or tri-furcate, largest individuals always at anterior end of chain. Length sporonts 100 to 150 $\mu$ , whole series attaining 1½ mm. Ratio LP: TL: :1:6 to 8; WP:WD: :1:1. First protomerite rounded at apex, wider than high, constriction at septum. Deutomerite elongate cylindrical, truncate at extremity. Epimerite a simple cylindrical knob. Nucleus spherical, one karyosome.

Cysts spherical, 100 $\mu$ . Dehiscence by rupture, spores ovoidal, 11 by 5 $\mu$ .

Intestine of *Limnobia* sp., larva; *Systenocerus caraboides* L. larva.

Taken in Poitou, France and in East Prussia.

#### Family ACTINOCEPHALIDAE Léger 1892: 166

#### Genus ACTINOCEPHALUS Stein 1848: 196

#### ACTINOCEPHALUS TIPULAE (Hammerschmidt) Léger

[Figure 6]

1838	<i>Bullulina Tipulae</i>	Hammerschmidt	1838: 357
1846	<i>Gregarina Tipulae</i>	Frantzius	1846: 28
1851	<i>Gregarina Tipulae</i>	Diesing	1851: 16
1859	<i>Gregarina Tipulae</i>	Diesing	1859: 739
1863	<i>Gregarina Tipulae</i>	Lankester	1863: 94
1892	<i>Actinocephalus tipulae</i>	Léger	1892: 141
1899	<i>Actinocephalus tipulae</i>	Labbé	1899: 26
1899	<i>Actinocephalus tipulae</i>	Léger	1899: 532
1903	<i>Actinocephalus tipulae</i>	Minchin	1903: 337
1911	<i>Actinocephalus tipulae</i>	Wellmer	1911: 130

Sporonts solitary, obese. Length nearly a millimeter. Width not given. Ratio LP:TL: :1:3.5 to 5; WP:WD: :1:1. Protomerite sub-spherical, widest in middle, deeply constricted at septum. Deutomerite widest at shoulder and tapers from thence to a rather short sharply pointed extremity. Epimerite not seen when alive and penetrating a cell, hence its supposed digitiform appendages not delineated. Portion seen a large round apically pointed papilla superimposed upon a short thick neck. Nucleus large, spherical. Several karyosomes.

Cysts spherical, 250 to 300 $\mu$  spores fusiform, 9 by 4 $\mu$ .

Intestine of *Tipula oleracea* L., larva, *Pachyrhina pratensis*, larva.

Taken in the Valley of the Vienne, France, and in East Prussia.

Diesing credits Hammerschmidt with having first seen and named this species. Since no data whatever exists concerning the species until Léger's time, it is doubtful that the two species are identical, especially since *Tipula* is parasitized by several gregarines, but the old record stands. Diesing gives as host *Ctenophora pectinicornis*, larva, in body cavity.

Léger places the species positively in the genus stated:

Ces caractères, (the epimerite as described above) joints à ceux fournis par la forme du sporadin du kyste et des spores, font rentrer, sans aucun doute, cette Grégarine dans le genre *Actinocephalus*.

#### ACTINOCEPHALUS sp. Léger

1899	<i>Actinocephalus</i> sp.	Léger	1899: 532
1903	? <i>Actinocephalus</i> sp.	Minchin	1903: 333

Host: *Ctenophora* sp., larva.

This species is not described, but merely mentioned in a list of other species found by Léger.

#### Genus SCHNEIDERIA Léger 1892: 153

Sporonts solitary. Protomerite separated from deutomerite by constriction but no septum (pseudomonocystid). Epimerite a flat disc with milled border, with or without central spine. Cyst dehiscence by simple rupture. Spores biconical, smooth. (It might be possible that a septum exists in the young trophozoites although this is not suggested by Léger.)

#### SCHNEIDERIA CAUDATA (von Siebold) Léger

[Figures 4 and 5]

1839	<i>Gregarina caudata</i>	von Siebold	1839: 51
1845	<i>Gregarina caudata</i>	Dujardin	1845: 638
1846	<i>Gregarina caudata</i>	Frantzius	1846: 23
1848	<i>Actinocephalus caudatus</i>	Frantzius	1848: 195
1851	<i>Gregarina caudata</i>	Diesing	1851: 8
1859	<i>Gregarina caudata</i>	Diesing	1859: 729
1863	<i>Gregarina caudata</i>	Lankester	1863: 94
1875	<i>Gregarina caudata</i>	Schneider	1875: 591
1892	<i>Schneideria coronata</i>	Léger	1892: 155
1899	<i>Schneideria caudata</i>	Labbé	1899: 22
1903	<i>Schneideria caudata</i>	Minchin	1903: 337, 199

Sporonts solitary, elongate. Maximum length 1 mm. Ratio LP:TL: : 1:9; WP:WD: :1.1:1. Protomerite flattened at apex, wider than high, widest in middle, constricted considerably to meet deutomerite but no septum present. Deutomerite long, slender, tapering from anterior end, a very long conical extremity. Epimerite a flattened disc with a milled border, no style in center, as in *S. mucronata*. Nucleus slightly ellipsoidal, one large karyosome.

Cysts not seen. Spores 20 by 10 $\mu$ .

Intestinal caeca of *Sciara nitidicollis* Meig., larva.

Taken in Poitou, France.



This parasite is one-fifth the length of its host, and because of the transparency of the host can easily be seen from without when both are alive.

No clue to the actual identity of this parasite exists in the earlier work except this by Diesing (1851):

Proboscis brevissime cylindrica apice subglobosa truncata crenata, uncinis retractus? which seems to apply to the epimerite. It seems strange, if this species is meant, that no one mentions the absence of a septum until Léger described anew the species with a new name. He does not refer to the earlier workers.

Labbé, however, unites the species under the older name. The hosts are identical.

### SCHNEIDERIA MUCRONATA Léger Type species

[Figures 1, 2 and 3]

1892	<i>Schneideria mucronata</i>	Léger	1892: 153
1899	<i>Schneideria mucronata</i>	Labbé	1899: 22
1903	<i>Schneideria mucronata</i>	Minchin	1903: 199, 333

Sporonts solitary, elongate. Length 700–800 $\mu$ . Width not given. Ratio LP:TL: :1:7; WP:WD: :1:1. Protomerite irregularly triangular, pointed, widest two-thirds its length from the apex. Deep constriction between protomerite and deutomerite. No septum. Deutomerite slender, gradually tapering from anterior end to a long slender point. Epimerite a wide flattened disc with a milled border and a short style in the center. Nucleus large, spherical, one karyosome. Very agile in movement, also polymorphic.

Cysts 270 by 190 $\mu$ , fusiform spores 15 by 9 $\mu$ .

Intestinal caeca of *Bibio marci* (L.), larva.

Taken in Tourraine and Poitou, France.

### SCHNEIDERIA sp. Léger

1899	<i>Schneideria</i> sp.	Léger	1899: 526, 532
1903	<i>Schneideria</i> sp.	Minchin	1903: 333

Very briefly described as unilocular, less than 250 $\mu$  in length, greatly dilated in the anterior portion and gradually tapering posteriorly. Epimerite not seen. Judging by context from similar parasites in other fly larvae, the author considers it a Polycystid rather than a Monocystid, which it resembles.

Host: *Chironomus* sp., larva.

Taken in Poitou, France.

### Genus STYLOCYSTIS Léger 1899: 529

Dicystid gregarine with a simple epimerite in form of a sharply pointed recurved spine. Spores biconical.



### STYLOCYSTIS PRAECOX Léger Type species

[Figure 33]

1899	<i>Stylocystis praecox</i>	Léger	1899: 529
1903	<i>Stylocystis praecox</i>	Minchin	1903: 199, 337
1911	<i>Stylocystis praecox</i>	Sokolow	1911: 283

Sporonts solitary, elongate, maximum length  $500\mu$ , width not given. Ratio LP:TL: :1:10. WP:WD: :1:1. Body cylindrical, somewhat dilated in anterior end. Tapering slightly at posterior end, end blunt. Nucleus spherical with one karyosome. Epimerite a slender recurved pointed spine.

Cysts elongate-ovoidal,  $200\mu$  in long axis. Spores biconical, 8 by  $5\mu$ .

Intestine of *Tanytus* sp., larva.

Taken at Grenoble, France.

### Genus TAENIOCYSTIS Léger 1906: 307

Deutomerite of sporont divided by septa into numerous segments one behind the other. Epimerite a small sphere set with six or eight recurved hooks. Spores biconical.

### TAENIOCYSTIS MIRA Léger Type species

[Figures 34 and 35]

1905?		Léger	1905: ?
1906	<i>Taeniocystis mira</i>	Léger	1906: 307
1908	<i>Taeniocystis mira</i>	Léger and Duboscq	1908a: 105
1911	<i>Taeniocystis mira</i>	Sokolow	1911: 284
1913	<i>Taeniocystis mira</i>	Ellis	1913: 280

Sporonts solitary, elongate cylindrical, deutomerite segmented, superficially resembling a tapeworm. Length  $400-500\mu$ . Width not given. Ratio LP:TL: :1:11. WP:WD: :1:1. Epimerite a relatively very small bulb with a corona of 6 to 8 recurved hooks set upon a short neck.

Cysts spherical,  $130\mu$ , spores 7 by  $3\mu$ .

Host: *Ceratopogon solstitialis* Winn., larva.

Taken at Cavaliere, France.

### Genus PILEOCEPHALUS Schneider 1875: 591

Epimerite a small lance-shaped or simple conoidal papilla placed unstalked upon the protomerite. Spores biconical.

### PILEOCEPHALUS STRIATUS Léger and Duboscq

[Figure 100]

1909	<i>Pileocephalus striatus</i>	Léger and Duboscq	1909b: 887
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Sporonts solitary, length  $150\mu$ . Protomerite more or less hemispherical, deutomerite broad, obtusely pointed. Epimerite a long striated bulb upon a short stout neck. Nucleus large, spherical, often found in the

protomerite (a phenomenon which has been nowhere else except in the species *Pileocephalus chinensis* by Schneider in 1886 and in *Acanthospora polymorpha* by Léger in 1897).

Cysts spherical.

Development extracellular, no cell destruction.

Intestine of *Ptychoptera contaminata*, larva.

Taken in Belgium?

LIST OF SPECIES FOUND IN THE ORDER SIPHONAPTERA OF  
THE CLASS HEXAPODA

PARASITE	Host
ACTINOCEPHALIDAE	
<i>Actinocephalus parvus</i> Wellmer	<i>Ceratopsyllus fringillae</i> (Wlk.)
	<i>C. gallinae</i> (Schrank), larvae
<i>Steinina rotunda</i> Ashworth and Rettie	<i>Ceratopsyllus styx</i> Roths.
GENUS OF UNCERTAIN POSITION	
<i>Agrippina bona</i> Strick.	<i>Ceratophyllus fasciatus</i> Bosc. larv.

Family ACTINOCEPHALIDAE Léger 1892: 166

Genus ACTINOCEPHALUS Stein 1848: 196

ACTINOCEPHALUS PARVUS Wellmer

[Figures 114 and 120]

1911 *Actinocephalus parvus* Wellmer 1911: 131

Sporonts ovoidal, maximum dimensions  $140\mu$  by  $75\mu$ . Ratio LP:TL: : 1:5; WP:WD: :1:1.3. Nucleus ovoidal, several karyosomes. Epimerite a corona of eight digitiform processes situated upon a short neck.

Cyst and spores unknown.

Intestine of *Ceratopsyllus fringillae* (Wlk.), larva (*Ceratophyllus f.*); and *C. gallinae* (Schrank), larva.

Taken at Königsberg.

Genus STEININA Léger and Duboscq 1904: 352

Epimerite a short mobile digitiform process changing into a flat button. Spores biconical.

STEININA ROTUNDATA Ashworth and Rettie

[Figures 121, 122, 123 and 124]

1912 *Steinina rotunda* Ashworth and Rettie 1912: 31

Sporonts solitary, obese to pyriform. No constriction at septum. Maximum dimensions  $180\mu$  by  $80\mu$ . Nucleus spherical, one or two large karyosomes.

Cysts spherical,  $110\mu$  to  $185\mu$  in diameter. Dehiscence by simple rupture. Spores ovoidal,  $12\mu$  by  $7\mu$ . Extracellular development. Intestine of *Ceratopsyllus styx* Roths. (*Ceratophyllus s.*)

Taken near Edinburgh.

## Genus of Uncertain Position

## AGRIPPINA Strickland 1912: 108

Sporonts solitary, epimerite a circular disc armed with digitiform processes on periphery, a short neck. Spores ellipsoidal.

## AGRIPPINA BONA Strickland 1912: 108 Type species

[Figures 101, 102, and 103]

1912 *Agrippina bona* Strickland 1912: 108

Sporonts elongate conoidal, average length 175 $\mu$ . Nucleus ellipsoidal. Protomerite dome-shaped, deutomerite tapering to a long pointed extremity from the shoulder. Epimerite as in genus.

Cysts spherical, dehiscing by rupture. Spores smooth, ellipsoidal, 6.6 by 7 $\mu$ .

Intestine of *Ceratophyllus fasciatus* Bosc., larva.

Taken at Cambridge, England.

## LIST OF SPECIES FOUND IN THE SUBPHYLUM TUNICATA

PARASITE	HOST
[? K��lliker]	<i>Phallusiae mamillaris</i> Ecker
[? Ritter]	<i>Perophora annectens</i>
[? Frenzel]	<i>Salpa maxima</i>
[? Roboz]	<i>Salpa confoederata</i> , <i>S. vagina</i>
[? Bargoni]	<i>Salpa aeruginosa</i>

[?K  lliker]

[Figure 55]

1848	<i>Gregarina phallusiae</i>	K��lliker	1848: 35
1848	<i>Stylorhynchus Phallusiae</i>	Frantzius	1848: 195
1851	<i>Gregarina Phallusiae</i>	Diesing	1851: 9
1859	<i>Gregarina Phallusiae</i>	Diesing	1859: 728
1863	<i>Gregarina Phallusiae</i>	Lankester	1863: 95
1899	<i>Pleurozyga phallusiae</i>	Lab��	1899: 49
1903	<i>Pleurozyga phallusiae</i>	Minchin	1903: 339

The figure given by K  lliker indicates the presence of a septum. Animal solitary, length 30 to 40 $\mu$ . Ratio LP:TL: :1:4.5. WP:WD: :1:1. Protomerite dome-shaped, constricted at septum. Deutomerite cylindrical, tapering slightly and ending in a broad, rounded extremity. Nucleus spherical. Epimerite a short bulbous style.

Cyst and spores unknown.

Taken at Triest.

Intestine of *Phallusiae mamillaris* Ecker.

The position of the gregarines in Tunicates is still uncertain. Little work has been done on them for thirty years and they offer an interesting

field from a phylogenetic point of view—both as regards the hosts and the parasites themselves. The Tunicates represent the highest type of hosts recorded for gregarines. Whether or not the gregarines are also the most complex is a problem of the future.

[? Ritter]

[Figure 98]

1893	<i>Gregarina</i> sp.	Ritter	1893: 69
1899	<i>Gregarina</i> sp.	Labbé	1899: 37
1903	<i>Gregarina</i> sp.	Minchin	1903: 339
1913	<i>Gregarina</i> sp.	Ellis	1913: 271, 290

40 $\mu$  in diameter. The parasites were found in the digestive tract, boring through the walls, and in the coelom. Three bands characterize all but the smallest, made up of "many elongated granules possibly cuticular in structure though they seem to take the stain."

Host: *Perophora annectens*.

The specimens described have little the character of polycystid gregarines (Fig. 98). There is a superficial resemblance to the genus *Taeniocystis*, but they possess no protomerite, and in one instance two nuclei are present, which leads to the hypothesis that they may belong to the genus *Haplozoon*.

[? Frenzel]

[Figures 39 and 117]

1885	<i>Gregarina Salpae</i>	Frenzel	1885: 565
1899	<i>Gregarina salpae</i>	Labbé	1899: 37
1903	" <i>Gregarina</i> " <i>salpae</i>	Minchin	1903: 339

Intestine of *Salpa maxima*.

[? Roboz]

1886	<i>Gregarina flava</i>	Roboz	1886: 1, 46
1899	<i>Gregarina flava</i>	Labbé	1899: 37
1903	" <i>Gregarina</i> " <i>flava</i>	Minchin	1903: 339

Intestine of *Salpa confoederata*, *S. vagina*.

[? Bargoni]

1894	<i>Gregarina ensiformis</i>	Bargoni	1894: 44
1899	<i>Gregarina ensiformis</i>	Labbé	1899: 37
1903	" <i>Gregarina</i> " <i>ensiformis</i>	Minchin	1903: 339

Intestine of *Salpa aeruginosa*.

The following data is given, by Bargoni, concerning this species:

Sospettai trattarsi di qualche parassita e particolarmente di una *Gregarina* avendone già altra, di forma però semilunare, ma molto simile pel contenuto giallognolo, avuta in esame dal Prof. Kleinenberg, che la trovò frequentemente parassita nella *Cydippe* e nella *Alciopa*. Di questa nuova forma, che non va confusa colla *Gregarina flava* del Roboz da me potuta osservare una volta sola in *Salpa aeruginosa*, mi occuperò altra volta, accontentandomi pel momento di distinguere col nome di *Gregarina ensiformis* n. sp.



## LIST OF HOSTS WITH THEIR GREGARINE PARASITES

HOST	PARASITE
<b>PLATYHELMINTHES</b>	
<i>Geoplana backi</i>	<i>Rhynchocystis geoplanæ</i> Fuhrman
<i>G. amagensis</i>	<i>Rhynchocystis geoplanæ</i> Fuhrman
<i>Planaria</i> sp.	<i>Lankesteria</i> sp. Swarczewsky
<i>Polyporus sulphureus</i>	Gregarine form, Wellmer
<i>Sorocoelis</i> sp.	<i>Lankesteria</i> sp. Swarczewsky
<b>ANNELIDA: Polychaeta</b>	
<i>Capitella capitata</i>	<i>Ancora lutzii</i> Hasselmann
<i>Clymenella torquata</i>	<i>Microtaeniella clymenellæ</i> Calkins
<i>Glycera siphonostoma</i>	<i>Gonospora glyceræ</i> Pixell-Goodrich
" "	<i>Gonospora intestinalis</i> Pixell-Goodrich
" "	Three unnamed parasites Pixell-Goodrich
<i>Ophelia neglecta</i>	<i>Rhytidocystis henneguyi</i> deBeauchamp
<i>Pareudrilus pallidus</i>	<i>Monocystis pareudrili</i> Cognetti de Martiis
" "	<i>Rhynchocystis hessei</i> Cognetti de Martiis
<i>Polydora ciliata</i>	<i>Polyrhabdina polydoræ</i> Caullery and Mesnil
<i>Polydora socialis</i>	<i>Doliocystis</i> sp. Faria, Cunha and Fonseca
" "	<i>Selendium cruzi</i> Faria, Cunha and Fonseca
<i>Pygospionis seticornis</i>	<i>Polyrhabdina pygospionis</i> Caullery and Mesnil
<i>Rhinodrilus incertus</i>	<i>Monocystis thamnodrili</i> Cogn. de Martiis
<i>Scolecopsis fuliginosa</i>	<i>Polyrhabdina spionis</i> Caullery and Mesnil
<i>Spio martinensis</i>	<i>Polyrhabdina brasili</i> Caullery and Mesnil
<b>ANNELIDA: Oligochaeta</b>	
<i>Kynotus Pittarellii</i>	<i>Taeniocystis legeri</i> Cogn. de Martiis
<i>Lumbricus terrestris</i>	<i>Monocystis rostrata</i> Muslow
" "	<i>Monocystis catenata</i> Muslow
<i>Lumbricus variegatus</i>	<i>Spirocystis nidula</i> Léger and Duboscq
<i>Glossoscolex wiengreeni</i>	<i>Monocystis perforans</i> Pinto
<b>ANNELIDA: Hirudinea</b>	
<i>Glossophonia complanata</i>	<i>Metamera schubergi</i> Duke
<i>Hemiclepsis marginata</i>	" "
<b>ROTIFERA</b>	
<i>Euchlanis dilatata</i>	<i>Monocystis minima</i> Konsuloff
<i>Salpina mucronata</i>	" "
<b>ECHINODERMATA</b>	
<i>Echinocardium cordatum</i>	<i>Lithocystis foliacea</i> Pixell-Goodrich
" "	<i>Urospora neapolitana</i> Pixell-Goodrich
" sp.	<i>Urospora echinocardii</i> Pixell-Goodrich
<i>Spatangus</i> sp.	<i>Urospora echinocardii</i> Pixell-Goodrich
<i>Synapta purpureus</i>	<i>Lithocystis microspora</i> Pixell-Goodrich
<i>Synapta galliennei</i>	<i>Urospora synaptæ</i> Cuenot
<i>Synapta digitata</i>	<i>Gonospora mercieri</i> Cuenot
<b>MOLLUSCA</b>	
<i>Cerithium vulgatum</i>	<i>Gonospora testiculi</i> Trébougoff

## CRUSTACEA

<i>Ampelisca spinipes</i>	<i>Cephaloidophora ampelisca</i> Kamm
<i>Anaspides tasmaniae</i>	<i>Ganymedes anaspidis</i> Huxley
<i>Atyephyra desmaresti</i>	<i>Uradiophora cuenoti</i> Mercier
<i>Balanus amphitrite</i>	<i>Pyxinoides bakani</i> Trégouboff
<i>Balanus eburneus</i>	<i>Pyxinoides balani</i> Trégouboff
" "	Unnamed parasite, Buddington
<i>Eriphia spinifrons</i>	<i>Porospora legeri</i> deBeauchamp
<i>Gammarus marinus</i>	<i>Cephaloidophora maculata</i> Léger and Duboscq
<i>Libinia dubia</i>	<i>Cephaloidophora olivia</i> Kamm
<i>Nephrops norvegicus</i>	<i>Porospora nephropsis</i> Léger and Duboscq
<i>Portunus depurator</i>	<i>Porospora maraisi</i> Léger and Duboscq
<i>Pisa gibosii</i>	<i>Porospora pisae</i> Léger and Duboscq
<i>Talitrus saltator</i>	<i>Cephaloidophora talitri</i> Mercier
<i>Talorchestia longicornis</i>	<i>Cephaloidophora delphinia</i> Kamm
<i>Uca pugnax</i>	<i>Cephaloidophora nigrofusca</i> Kamm
<i>Uca pugilator</i>	

## CHILOPODA

<i>Scelopendra heros</i>	<i>Amphorocephalus amphorellus</i> Ellis
" <i>subspinipes</i>	<i>Nina indicia</i> Merton
" sp.	<i>Echinomera magalhãesii</i> Kamm
" sp.	<i>Seticephalus elegans</i> Kamm
" sp.	<i>Gregarina brasiliensis</i> Pinto
<i>Scelopendrella</i> sp.	Gregarine form, Wellmer

## DIPLOPODA

<i>Callipus lactarius</i>	<i>Stenophora lactaria</i> Watson
<i>Euryurus erythropygus</i>	<i>Stenophora diplocorpa</i> Watson
<i>Fontaneria coarctata</i>	<i>Stenophora caudata</i> Watson
<i>Orthomorpha coarctata</i>	<i>Stenophora elongata</i> Ellis
" <i>gracilis</i>	<i>Stenophora robusta</i> Ellis
" sp.	" "
" sp.	<i>Fonsecaia polymorpha</i> Pinto
<i>Parajulus impressus</i>	<i>Stenophora impressa</i> Watson
" <i>venustus</i>	<i>Stenophora robusta</i> Ellis
" sp.	<i>Stenophora cockerellae</i> Ellis
<i>Rhinocricus pugio</i>	<i>Stenophora cunhai</i> Pinto
" sp.	<i>Stenophora lutzii</i> Pinto
" sp.	<i>Stenophora cruzi</i> Pinto
" sp.	<i>Stenophora viannai</i> Pinto
" sp.	<i>Stenophora umbilicata</i> Pinto
" sp.	<i>Stenophora tenuicollis</i> Pinto

## THYSANURA

<i>Sminthurus fuscus</i>	Gregarine form, Wellmer
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## ORTHOPTERA

<i>Ceuthophilus latens</i>	<i>Gregarina longiducta</i> Ellis
" <i>maculatus</i>	<i>Gregarina longiducta</i> Ellis
" <i>neglectus</i>	<i>Gregarina neglecta</i> Watson
" <i>stygius</i>	<i>Gregarina stygia</i> Watson
" <i>valgus</i>	<i>Gregarina consobrina</i> Ellis

*Conocephalus frater*  
*Encoplotophus sordidus*  
*Forficularia auricularia*  
*Gryllus abbreviatus*  
*Ischnoptera pennsylvanicus*  
*Melanoplus differentialis*  
 " *femur-rubrum*  
*Udeopsyllae nigra*

## HEMIPTERA

*Spiniger* sp.

## NEUROPTERA

Aeschnidae lv.  
*Aeschna* sp.  
*Phryganea grandis*  
*Sympetrum rubicundulum*  
*Tramea lacerata*

## DIPTERA

*Anopheles bifurcatus* lv.  
*Aphiochaeta rufipes* lv.  
*Ceratophyllus fasciatus*  
*Ceratopsyllus farreni*  
 " *fringillae* lv.  
 " *gallinae* lv.  
 " " ad.  
 " *styx*  
*Ficallbia dofleini* lv.  
*Simulium bracteatum* lv.  
*Stegomyia fasciata* lv.

## COLEOPTERA

*Alobates pennsylvanicus*  
*Amara angustata*  
*Asida opaca*  
*Asida* sp.  
*Broscus cephalotes*  
*Carabus* sp.  
*Clerid* lv.  
*Coccinella* sp.  
 " sp.  
*Coccinella novemnotata*  
*Coptotomus interrogatus*  
 " "  
*Crypticus quisquilius*  
*Cucujus* lv.  
*Cychrus rostratus*  
*Dermestes lardarius*  
*Diabrotica vittata*  
*Elateridae* lv.  
*Eleodes* sp.  
*Eusallus* sp.

*Gregarina chagasi* Pinto  
*Gregarina nigra* Watson  
 Gregarine form, Pantel  
*Gregarina galliveri* Watson  
*Gregarina illinensis* Watson  
*Gregarina nigra* Watson  
 " "  
*Gregarina udeopsyllae* Watson

*Schizocystis spiniger* Machado

*Bothriopsis claviformis* Pinto  
*Actinocephalus brachydactylus* Ellis  
*Diplocystis phryganeae* Berg-von-Emme  
*Prismatospora evansi* Ellis  
 " "

*Caulleryella anophelis* Hesse  
 " *aphiochaetae* Keilin  
*Agrippina bona* Strickland  
*Steinina rotundata* Ashworth and Rettie  
*Actinocephalus parvus* Wellmer  
*Actinocephalus parvus* Wellmer  
*Steinina rotundata* Ashworth and Rettie  
 " "  
 Unnamed par. Guenther  
 Unnamed par. Strickland  
*Lankesteria culicis* Stevenson and Wenyon

*Actinocephalus zophus* Ellis  
*Steinina rotunda* Watson  
*Stylocephalus giganteus* Ellis  
*Stylocephalus giganteus* Ellis  
*Gregarina erecta* Wellmer  
*Cometoides* sp. Wellmer  
*Bulbocephalus wardi* Watson  
*Gregarina fragilis* Watson  
*Gregarina katherina* Watson  
 " "  
*Gregarina globosa* Watson  
*Gregarina coptotomi* Watson  
*Gregarina ovoidea* Wellmer  
*Bulbocephalus elongatus* Watson  
 Gregarine form, Wellmer  
*Pyxinia bulbifera* Watson  
*Gregarina diabrotica* Kamm  
*Gregarina gracilis* Watson  
*Stylocephalus giganteus* Ellis  
 " "

<i>Harpalus aeneus</i>	<i>Gregarina polyaulia</i> Wellmer
<i>Harpalus pennsylvanicus</i>	<i>Actinocephalus gimbeli</i> Watson
“ “ <i>erythropus</i>	<i>Hirmocystis harpali</i> Watson
“ “ <i>longior</i>	<i>Steinina harpali</i> Watson
<i>Harpalus ruficornis</i>	<i>Gregarina polyaulia</i> Wellmer
<i>Heledona agricola</i>	Gregarine form, Wellmer
<i>Helophorus aquaticus</i>	<i>Monocystis</i> sp. Wellmer
<i>Hydrophilus aterrimus</i> lv.	Cometoides-like form, Wellmer
“ sp.	<i>Bothriopsis terpsichorella</i> Ellis
<i>Hyllobius abietis</i>	<i>Gregarina hylobii</i> Kamm
<i>Ips typographus</i>	<i>Gregarina typographi</i> Fuchs
<i>Lagria hirta</i>	<i>Gregarina rostrata</i> Wellmer
<i>Leptochirus edax</i>	<i>Actinocephalus crassus</i> Ellis
“ “	<i>Stylocystis ensiferus</i> Ellis
<i>Ninus interstitialis</i>	<i>Gregarina guatemalensis</i> Ellis
<i>Nyctotheres barbarata</i>	<i>Actinocephalus zophus</i> Ellis
<i>Omoplatia normalis</i>	<i>Gregarina watsoni</i> Pinto
<i>Platydemia excavatum</i>	<i>Gregarina platydema</i> Kamm
<i>Platynus ruficollis</i>	<i>Gregarina platyni</i> Watson
<i>Procrustes coriaceus</i>	<i>Actinocephalus permagnus</i> Wellmer
<i>Pterostichus niger</i>	<i>Gregarina exiguus</i> Kamm
“ “	<i>Actinocephalus echinatus</i> Wellmer
<i>Pterostichus stygicus</i>	<i>Gregarina monarchia</i> Watson
“ “	<i>Gregarina intestinalis</i> Watson
“ <i>vulgaris</i>	<i>Actinocephalus echinatus</i> Wellmer
<i>Systema</i> sp.	<i>Gregarina aragaoi</i> Pinto
<i>Tenebrio castaneus</i>	<i>Gregarina grisea</i> Ellis
<i>Tenebrionidae</i> lv.	<i>Gregarina tenebrionella</i> Watson
<i>Tribolium ferrugineum</i>	<i>Gregarina minuta</i> Ishii
“ “	<i>Gregarina crassa</i> Watson
“ “	<i>Didymophyes minuta</i> Kamm
“ “	<i>Steinina obconica</i> Ishii
<i>Tritoma quadripustulata</i>	Gregarine form, Wellmer

## LEPIDOPTERA

<i>Endrosis fenestrella</i> lv.	<i>Leidyana tinei</i> Keilin
<i>Oecophora pseudopretella</i>	Unnamed Gregarine
<i>Tinea pallescentella</i>	Unnamed Gregarine

## ARACHNIDA

<i>Ctenocephalus serraticeps</i>	<i>Gregarina ctenocephalus</i> Ross
<i>Oribata geniculata</i>	<i>Gregarina</i> sp. Wellmer

## TUNICATA

<i>Stolonica socialis</i>	<i>Selysina perforans</i> Duboscq
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## ENTEROPNEUSTA

<i>Glossobalanus minutus</i>	<i>Selenidium metchnikovi</i> Léger and Duboscq
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### EXPLANATION OF PLATES

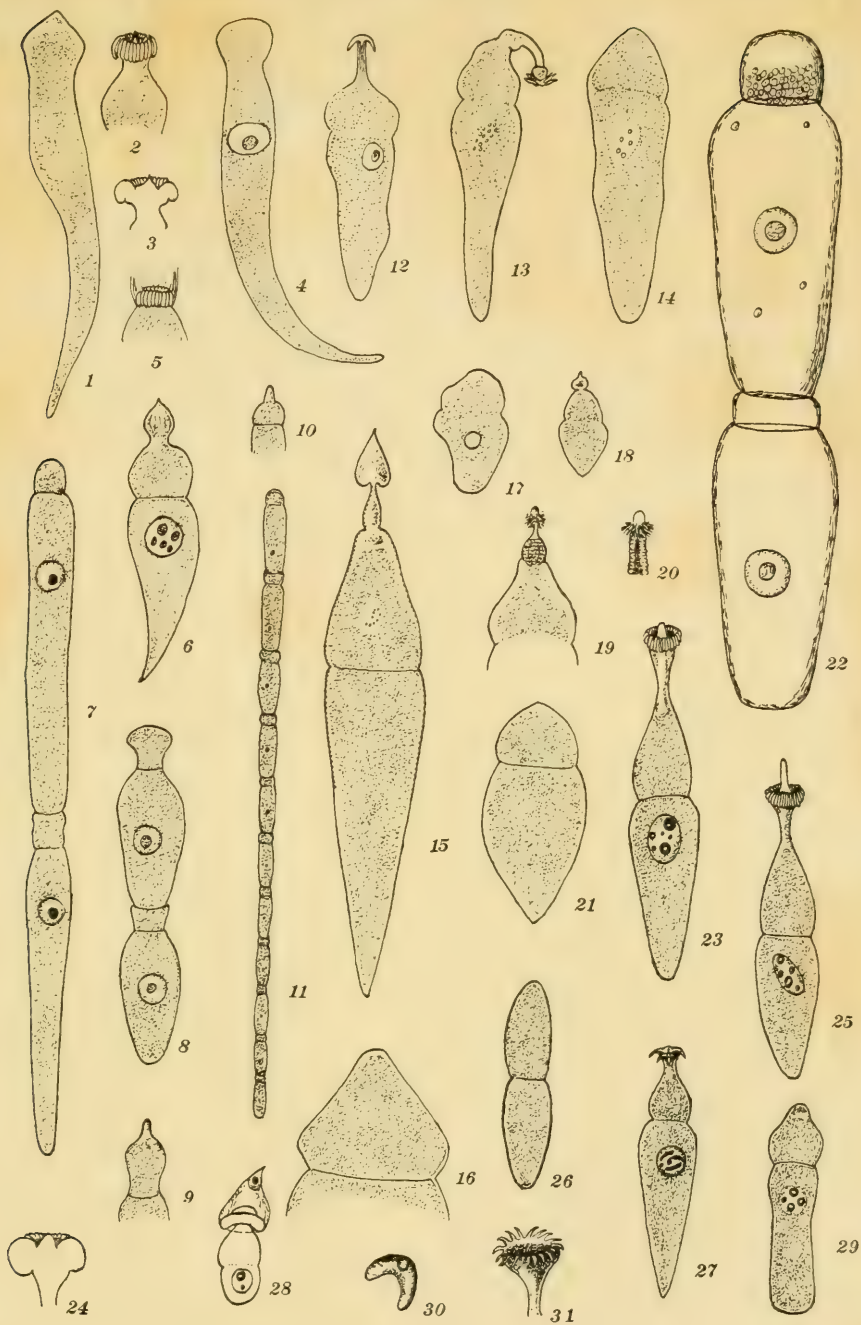
Drawings were either traced directly from the author's plates or enlarged by means of the camera lucida. Magnifications are not given for they did not appear in most of the original sources. The text will furnish the exact size of each species so far as data were available in the original publication or in the later articles.

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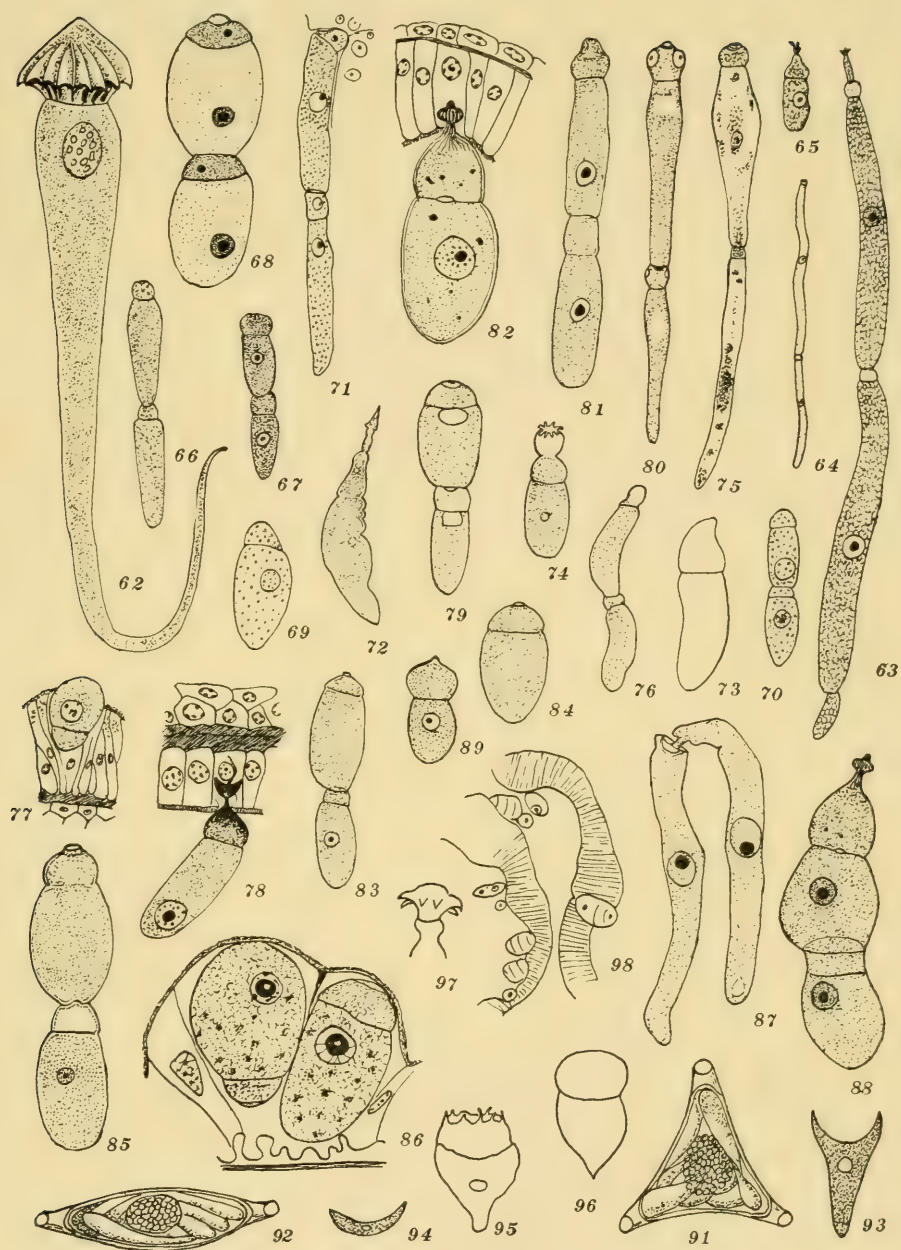


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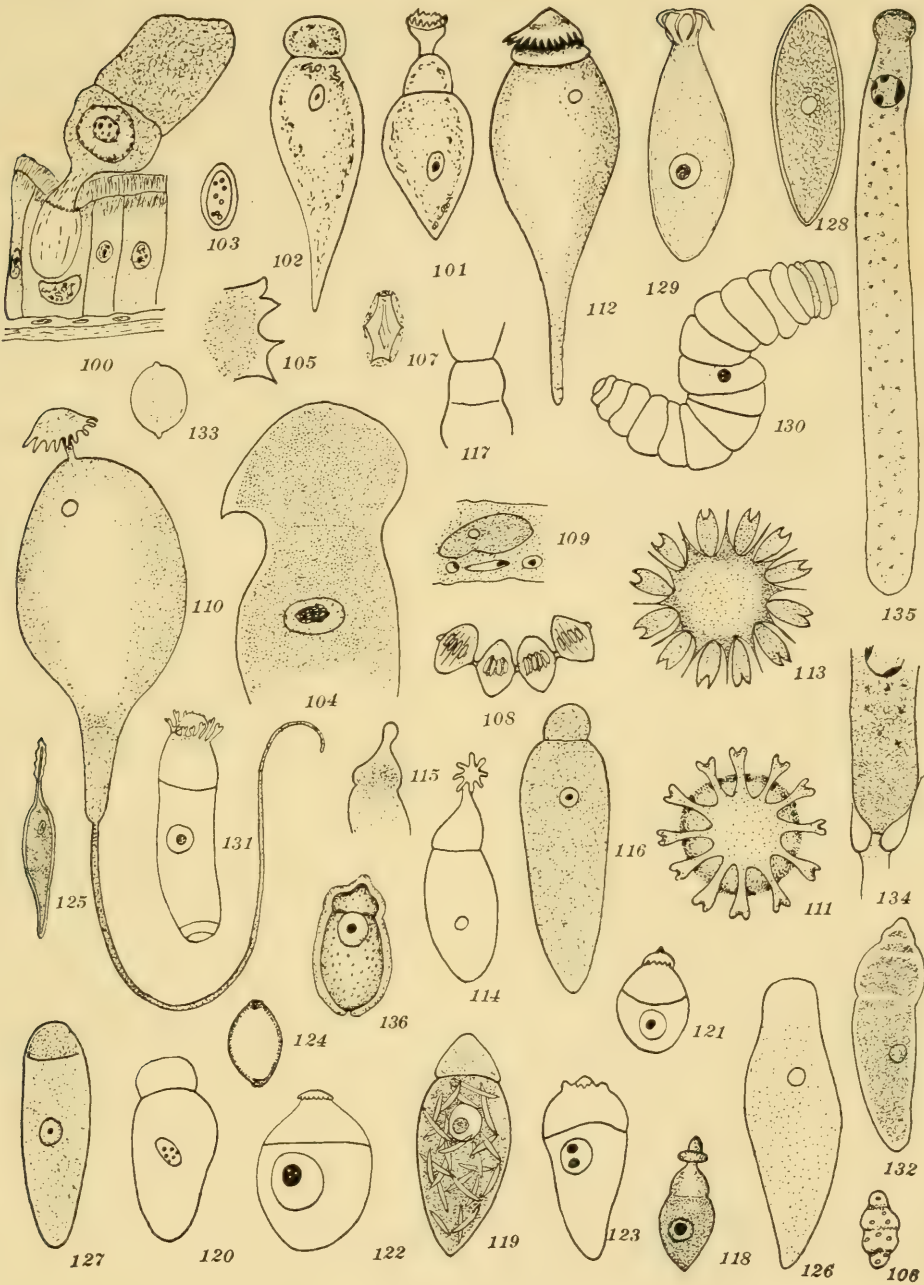


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THE MOLLUSCAN FAUNA OF THE  
BIG VERMILION RIVER,  
ILLINOIS

With Special Reference to its Modification as the Result of  
Pollution by Sewage and Manufacturing Wastes

WITH FIFTEEN PLATES AND ELEVEN TABLES

BY  
FRANK COLLINS BAKER  
Curator of the Museum of Natural History  
University of Illinois

Contributions from the  
Museum of Natural History of the University of Illinois  
No. 22



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## INTRODUCTION

The present paper embodies the result of investigations of the mollusk fauna of one of the smaller rivers of the State of Illinois, the Big Vermilion, carried on during the years 1918 to 1920. To this are added notes on another river, the Sangamon, for comparison. While all groups of mollusks were considered, special emphasis has been placed on the Unionidae or pearly fresh water mussels (*Naiades*), on account of their abundance, their significance in matters of geographic distribution, and their importance from an economic standpoint, as raw material from which pearl buttons are made.

For a number of years, the United States Bureau of Fisheries has been engaged in conducting a series of investigations of several rivers of Illinois and Indiana, for the purpose of ascertaining the mussel resources of these streams. In view of the rapid depletion of the supply in the larger rivers (Mississippi, Ohio, Illinois) it becomes necessary to search the smaller streams to replenish the older beds. The Maumee and the Kankakee (Wilson and Clark, 1912), as well as the Illinois (Danglade, 1914), have recently been rather carefully surveyed with interesting and important results.

It was thought that a somewhat similar investigation of the Big Vermilion River would be of value. The scope of the investigation included everything that appeared to affect the molluscan life of the river, physical characters, pollution, general relation and number of species. It was believed, also, that the Big Vermilion, as well as other smaller streams in the State, might provide good breeding stock with which to carry on artificial glochidial infection of fish, and the results seem to warrant the assumption. It will be necessary to make more or less detailed surveys of all of the smaller rivers and their tributaries, and the present paper may be considered a contribution toward this end, covering fully the Big Vermilion from its upper waters to the vicinity of Danville, a distance of about forty-five miles by stream. A portion of the Sangamon is considered, and this river may also prove a valuable source of mussel material.

Little has been done by field naturalists in the study of the distribution of the molluscan fauna of a stream from the headwaters to the larger portions of these rivers. Perhaps the most thorough and notable study of this character was carried on by Adams (1900, 1915), on the genus *Io* in which the Tennessee River and its tributaries (Powell, Clinch, Holston, French Broad, Nolichucky, etc.) were studied from sources to Chattanooga.

Ortmann has made a study of the distribution of the Naiades in the streams of Tennessee from this standpoint, using material collected by Adams (Ortmann, 1918); and Wilson and Clark (1912) have added greatly to our knowledge of the comparative distribution of the mussel faunas of the Kankakee and Maumee rivers.

Studies of this kind bring out the fact that certain species are characteristic of the upper reaches of a stream while others are found only in the lower part. Barriers, such as falls and polluted water, are also seen to have a large influence on the distribution of mollusks, especially river mussels. The same species may also vary in size or shape in different parts of the stream, as noted by Ortmann (1920). In fact, a true picture of the characteristics of the fauna of a river or smaller stream can be gained only by this method, which the present paper clearly shows.

The Salt Fork of the Big Vermilion is a striking example of the ill effect of sewage and other pollution on the fauna of a stream. It was carefully studied from this standpoint in order to determine accurately the distance that the polluted stream must flow before a normal fauna can establish itself, and to ascertain the relative effect of pollution on different species of mussels as well as on other aquatic animals. Mussels and crayfishes are considered good indicators of the measure of pollution in a stream and the absence of both of these groups of animals from the upper part of the Salt Fork is ample evidence of the septic condition of this stream.

The work was largely carried on during the months of August, September, and October, when the water was low. Collecting was done by wading in the stream as deep as hip rubber boots would permit. In the shallow water (up to two feet in depth) the entire bottom was gone over with the hands, and the mussels and other mollusks thus picked from the bottom of mud, gravel, and sand. Samples of all mollusks, as well as associated animals of the other groups, have been preserved in the Natural History Museum of the University of Illinois.

The different areas of the region studied are covered by three maps of the United States Geological Survey, the Mahomet, Champaign, and Danville Folios, and on these the stations recorded in this paper may easily be located.

#### ACKNOWLEDGMENTS

The writer is greatly indebted to Professor Frank Smith, not only for invaluable assistance in collecting much of the material upon which the paper is based, but also for many notes on the distribution of the Naiades and other mollusks in the two river systems. Professor Smith has studied the fauna of the Salt Fork and the Sangamon streams for many years, collecting from them at different times of the year. His classes in zoology have visited Homer Park yearly for a long period and thus the mollusk

fauna of this locality is better known than that of any other part of the stream.

To Professor Smith the writer is also indebted for the identification of the worms and crayfish, and the determination of the animal life in the samples of bottom sludge from the polluted part of Salt Fork. The sincere thanks of the writer are due to the persons noted below; the group of animals or plants which they have identified is indicated: Dr. Charles P. Alexander, *Coleoptera* and other insects; Dr. Edward Bartow; Dr. Stephen A. Forbes; Mr. Calvin Goodrich, *Goniobasis*; Dr. George M. Higgins; Mr. John Malloch, *Diptera*; Dr. J. Percy Moore, *Hirudinea*; Professor James E. Smith; Dr. E. N. Transeau, *Algae*; Dr. Victor Sterki, *Sphaeriidae*; Dr. Harley J. Van Cleave; Dr. Bryant Walker, *Ancylidae* and other mollusks.



## PHYSICAL FEATURES OF THE BIG VERMILION BASIN

The Big Vermilion River drains about 1,500 square miles in Champaign, Ford, and Vermilion counties in Illinois and a small portion of Warren and Fountain counties, Indiana. The North Fork also drains from a small territory in the southeastern part of Iroquois County, Illinois. The main stream, known as Middle Fork, rises in the southern part of Ford County near the town of Melvin, in the Bloomington morainic system, at a height of 800 feet above sea level. Its course is southeastward, between the hills of the moraine known as the Roberts and Melvin ridges, passing through the latter and uniting with a tributary known as the West Branch of the Middle Fork, which also rises at an elevation of 800 feet in the Roberts ridge. At Potomac, the stream turns southward, cuts through the outer ridge of the Bloomington moraine and crosses the plain of the Champlain till sheet, uniting with the Salt Fork about six miles west of Danville.

The largest western tributary, known as the Salt Fork, rises in the till plain in the north-central part of Champaign County, near Thomasboro, at an elevation of about 740 feet above the sea. It drains the till plain lying between the Bloomington moraine on the north and the Champaign moraine on the south. It flows in a south and east direction for about 55 miles<sup>1</sup> and unites with the Middle Fork as described above. A large tributary of Salt Fork, known as Spoon River<sup>2</sup> rises in the northeastern part of Champaign County, in two branches, not far from the outer ridge of the Bloomington moraine. Its general course is southward for a distance of about ten miles, where it unites with the Salt Fork near St. Joseph.

Another large tributary is known as the North Fork, which rises in the southeastern corner of Iroquois County in the inner ridge of the Bloomington moraine. It flows southward, cutting through the middle and outer ridges of the moraine, crosses a part of the Champaign till plain and unites with the Big Vermilion at Danville. This tributary has a length of about 40 miles. From Danville the larger stream flows southeastward for about 20 miles, crossing a part of Vermilion County, Indiana, and empties into the Wabash River 10 miles from the Illinois State line.

The basin of the Big Vermilion River lies in or is surrounded by glacial moraines of the Early Wisconsin glaciation, the Bloomington moraine on

<sup>1</sup> Length of rivers designates total length including all meanders.

<sup>2</sup> Not to be confounded with Spoon River entering the Illinois River near Havana, Mason County.

the north and the Champaign moraine on the south. In its course it cuts through the Bloomington moraine in several places. The territory drained includes a small part of the Bloomington till plain and a considerable part of the Champaign till plain (Leverett, Illinois Glacial Lobe, plate VI.) As there are no outcroppings of rock in this area the streams have cut well defined, though meandering, channels. The upper, small, creek-like tributaries have sunk their beds but a few feet below the general level of the country, but lower down, the stream, after receiving several large tributaries, has cut its bed to a depth of ten or fifteen feet. In Middle Fork and North Fork, and in the Big Vermilion from above Middle Fork to the Wabash, the river has cut deep canyons upwards of 200 feet in depth, which produce some of the most picturesque scenery in the State of Illinois. This river valley varies from half a mile to a mile in width and in one place, about four miles below Danville, it widens to form a large amphitheater two miles wide and a mile long, with cliffs and hills rising on all sides to a height of over 150 feet.

Outside of the stream valleys the country is a flat till plain, largely devoted to crop purposes. Ridges, made up of the Champaign and Bloomington moraines and their branches, occur and have been largely instrumental in directing the course of some of the stream drainage. The Salt Fork turns to the north after leaving Urbana, and passes around Yankee ridge (a branch of the Champaign moraine) near the Brownfield woods, and spurs from the Champaign moraine occur in several places on the west and south banks of the Salt Fork, which are relatively high and the stream skirts their bases.

The bottom of the main stream and its tributaries varies greatly. The small tributaries mostly have mud bottoms. In Spoon River the bottom is of mud in most places and the water is of considerable depth, even in summer (three to four feet maximum in August). In places there are riffles where the water is very shallow (a foot or less) and the bottom here is of sand and fine gravel. The Salt Fork below St. Joseph is made up of stretches of stream where riffles with sand and gravel bottom alternate with deeper back water with mud bottom. Near Muncie there are outcrops of rock, a small tributary, Stony Creek, flowing over a stony bed. In the Middle Fork, shale rock outcrops in several places, notably below the interurban bridge, where the whole bottom is composed of a sheet of rock with a thin coating of sediment in spots. The same conditions are found in parts of the North Fork and in the Big Vermilion. These varying conditions provide the most favorable environment for the growth of river mussels, a fact made evident by the large naiad fauna found in the stream despite the unfavorable effects of sewage and waste pollution.

Natural dams occur in a few places in the Salt Fork, caused by the accumulation of débris which has lodged against the trunk of a tree that

has fallen across the stream. At Homer Park, an artificial dam about five feet in height causes slack water for several miles up the stream. This dam markedly affects the mollusk fauna, the tumbling of the water over the dam mixing air with the polluted water and providing the dissolved oxygen so necessary to naiad life. It is probable that the large number of species of mussels found at some stations above this dam is due largely to the presence of sections of the stream where riffles provide the oxygenating agent. Mussels were usually found in or near such habitats. The mussel fauna below the Homer Park dam numbers 28 species while above the dam, as far up stream as Sidney, only 17 species occur, 10 species not passing the barrier, although the environment does not differ essentially. The current in the river is rapid over the riffles but rather sluggish in the deeper places. The difference between high and low water (spring and fall) is about six feet. The streams usually vary in width from ten to thirty feet.

In the late summer and fall the small tributary streams (creeks and rivulets) flowing into Salt Fork and other branches of the Big Vermilion are usually either dry or contain scattered pools of water throughout their length. They do not contribute any water, therefore, to the larger stream at this time of the year. The mollusks living in these tributaries bury themselves in the mud during this period of dry bottom and hibernate. Many die at this time.

The banks of the stream valleys, exclusive of the small tributaries, are for the most part high and well wooded especially where the valley floor is wide enough to permit meandering, in which cases the flat floodplains are abundantly wooded. These flat areas vary from a few hundred feet to a half mile in width. About two miles above Sidney an island has been formed by the forking of the stream, the area embraced being about 650 by 1200 feet. At this place the right bank is 20 feet high and the left bank quite low. The presence of fossil shells indicates that the island was probably the result of silt accumulation during a long period of time. The wooded banks of the stream alternate with farm lands, some in pasture and others in crops. Many of the crop lands have a fringe of timber bordering the stream. That the stream is high and powerful during the spring when it is in flood is evidenced by the tangled mass of logs and other woody debris which thickly cover the flood plain areas along the valley. Such conditions were especially noted between Sidney and Homer Park.

The current varies somewhat, being relatively sluggish in the backwater above dams and riffles, but quite swift over the shallow places. During the flood periods of spring and early summer the current is quite swift and in places becomes torrential. This condition is indicated by the large number of trees which have been thrown on the flood plains far above the margin of low water. As measured during the month of October the current in the Salt Fork at Urbana and a few miles down the stream had a velocity



of from half a mile to a mile an hour. The water was very low when these measurements were taken by the State Water Survey. In its course of 90 miles to the Wabash River, the Big Vermilion River falls about 320 feet or  $3\frac{1}{2}$  feet per mile. It thus has a greater fall than either the Kankakee, which is 300 miles long and has a fall of 250 feet, or less than a foot per mile, or the Maumee River, which has a length of 150 miles and a fall of 154 feet, or about a foot per mile (Clark and Wilson, 1912).

The water in the normal parts of the stream is usually clear at depths of one to two and a half feet, especially on the riffles. This condition was noted in Salt Fork east of Sidney, and in the Middle Fork. Above Sidney, except where the water is very shallow, the stream is murky and laden with fine silt. During times of high water the stream is in this condition in all parts of the Big Vermilion. The upper part of Salt Fork, from Urbana to a point six or eight miles down stream is always more or less brownish in color from the large amount of sewage, equalling as much as a third of the total volume, and putrient matter as well as an oily scum is usually to be seen on the surface. The shore of the stream is rendered very unsightly by the mass of filth that is despoiled above the usual level by high water. At St. Joseph, ten miles from Urbana, much the same condition is found.

The upper part of the Salt Fork has been greatly modified by ditching and dredging. North of Urbana for the distance of a mile and a quarter above Crystal Lake Park a large ditch carries the surface drainage in a straight line to the park thus cutting off the tortuous windings of the original stream bed, which have been left as long, narrow, shallow ponds, reminding one of the 'ox-bows' so common in the valley of the Mississippi River. The bed of this ditch is about six feet below the general level of the surface. For several miles above this ditch the original stream has been deepened by dredging and the bed is now pretty generally five or six feet lower than that of the original stream.

From Crystal Lake Park, Urbana, to a point near St. Joseph, the stream has been ditched to straighten the bed, leaving numerous 'cut-offs' of the old stream bed. This canal permits a better flow of water for the disposal of the sewage. Where not ditched the stream bed has been deepened. The ditching has greatly modified the original stream bed, providing a new and different kind of environment for the mussels and other aquatic life. It is probable that all of the old fauna was exterminated during the ditching operations and the sewage pollution provides an unfavorable environment, which the aquatic bottom life does not seem able or inclined to enter. The effect of sewage pollution may be seen all the way down the stream from the source of contamination. At St. Joseph, where the stream bed has not been modified, conditions are very bad, the mud in the bottom being filled with gas forming bacteria which are constantly causing bubbles of gas to break at the surface of the water. Were it not for the sewage pollution, the stream



at this place would be quite normal for the life of mussels and other bottom animals. (See the chapter on sewage pollution.)

Several other river systems have their beginning near Urbana and Champaign, on the southwest side of the Champaign moraine. These are the Embarras, which has tributaries rising south of Urbana; the Kaskaskia, which has its inception northwest of Champaign near the village of Rising; the Little Vermilion, which rises in the southeastern part of Champaign County; and the Sangamon, which rises in the extreme northwestern part of Champaign County not far from Gibson. Only the last stream has been examined for its mussel fauna for the purpose of making comparisons with the fauna of the Big Vermilion River.

The Sangamon River has a length of about 180 miles and a drainage basin of some 5670 square miles. It rises on the south side of the Bloomington moraine in McLean County, "at an elevation of 850 feet above sea level, and cuts through two moraines in its course, the Champaign and the Shelbyville. The river channel is tortuous and meandering and the flood plain in many places very wide. The banks of the stream are low for the most part and wooded in spots. The stream has been examined carefully at only two points, Mahomet and west of White Heath, the first locality receiving the most attention. Near Mahomet the river is notably meandering, the banks are high, the Champaign moraine rising 90 feet above the water level near the village. The river bank is usually five or six feet above the stream, which has cut vertical cliff-like banks in many places. Below Mahomet the woodlands are abundant, extending well back from the river in some places. The river varies in width from 40 to 50 feet. The bottom alternates between riffles with sand and gravel bottom and deeper back water stretches with mud bottom. The former habitats are a foot or so in depth and the latter habitats two to four feet in depth in the summer. In the spring the river is ten to twelve feet deep and very swift, at times becoming torrential. The average fall of the stream is 2.3 feet per mile. Many logs and other débris thrown up on the flood plains attest the power of the river during spring floods.

West of White Heath, for a mile above the I. C. railroad bridge to two miles below, the river has been examined, though no systematic collecting comparable to that carried on at Mahomet has been done. The stream in the portion of the river valley examined is similar to that near Mahomet in its general physiographic features. The banks of the stream are on the whole lower than farther up the river near Mahomet. Studies of this stream similar to those carried on in the Big Vermilion and its tributaries would doubtless yield interesting and valuable results. The Sangamon is a characteristic mussel stream and should contain a much larger mussel fauna than at present known and listed.

## GENERAL BIOLOGY OF THE BIG VERMILION RIVER

Although the chief purpose of the study of this stream was to ascertain the general conditions and distribution of the fresh water Mollusca, especially the Naiades or river mussels, such attention was given to other groups as came easily under observation. At least one of these groups bears an intimate relation to the Naiades in the matter of distribution as restricted by pollution, e.g., the crayfishes, and another, the fish, is closely related to the breeding habits of the mussels. Others, as some of the oligochaete worms, are especially characteristic of polluted waters. A few notes are given under each group.

The Protozoa and other microscopic groups are omitted because given little or no attention, except in the polluted part of Salt Fork. These are mentioned in the section on sewage pollution. The Big Vermilion and its tributaries present a wide field for the study of other kinds of aquatic life that are especially characteristic of the upper reaches of a river system

### PLANTS

The larger aquatic plants were notably scarce in most parts of the Salt Fork. In several places in Salt Fork, especially near Sidney, between the cement and railroad bridges, the shores are lined with the spatterdock, *Nymphaea advena* Ait (see Fig. 11). The cat-tail, *Typha latifolia*, Linn., is common in various stretches of the stream, bordering the shore. The arrow-head, *Sagittaria latifolia* Willd., and the larger blue flag, *Iris versicolor*, Linn., were observed along the shore in many places. The water willow, *Dianthera americana* Linn., is abundant in the shallows in many parts of the Salt Fork below Homer Park. *Elodea canadensis* Michx., was abundant at Homer Park.

Filamentous algae occurs in many places, attached to submerged objects. Among these *Cladophora* and *Spirogyra* were noted. Septic algae growing in the polluted portion of Salt Fork are noted under the section on pollution of the stream.

### WORMS

Nematoda. *Gordius robustus* Leidy, was collected in several places in Salt Fork between the first bridge below St. Joseph and the bridge above Sidney. It was found in mud bordering the shore, in shallow water. A number of minute nematodes were observed in the sludges of the bottom in Salt Fork between Urbana and St. Joseph. These were not identified.

Oligochaeta. These aquatic earthworms were abundant in places along the shore of Salt Fork. *Sparganophilus eiseni* Smith occurred in abundance in the mud on the margin of Salt Fork at Homer Park, and immature worm of this genus, as well as cocoons, were collected from near the bridge below St. Joseph to the bridge above Sidney. A single specimen of *Helodrilus chloroticus* (Savigny) was collected in the Salt Fork near St. Joseph. This species has not heretofore been recorded from Illinois and its occurrence at this locality adds another species of earthworm to the State list (see Smith, 1915:557). *Limnodrilus* was abundant in bottom sludges from the Salt Fork, from Urbana to near St. Joseph. *Tubifex* was also found, but not as abundantly.

Hirudinea. Two species of leeches occurred in several places in Salt Fork, below St. Joseph. They were nowhere abundant. The two species are: *Erpobdella punctata* (Leidy) Moore and *Placobdella rugosa* (Verrill) Moore.

#### CRUSTACEA

Three species of crayfish (*Cambarus*) were determined by Professor Smith from the material collected in Salt Fork and other parts of the Big Vermilion River. The most abundant was *Cambarus propinquus* Girard, which was found commonly from bench mark 655 to the Big Vermilion River below Middle Fork. It is especially abundant in the latter place where an individual may be found under every piece of stone. The same species was abundant in Stony Creek and in the Salt Fork near Muncie.

*Cambarus blandingi acutus* Girard, both young and adult, occurred in the upper parts of Salt Fork, but preferred a mud bottom rather than a rock bottom. *Cambarus immunis* Hagen was collected only at bench mark 655 where it was rare.

It will be noted that *Cambarus* is first met with about two miles below St. Joseph and twelve miles from Urbana. The only ones seen here were dead. Living crayfish begin to appear in abundance about six miles below St. Joseph or sixteen miles below Urbana. Crayfish and mussels both become common or abundant at about the same time, viz., fourteen and sixteen miles below the source of sewage pollution at Urbana. This agreement in distribution indicates the close relationship between these otherwise diverse groups of animals, as regards resistance to septic conditions, neither being able to thrive under pollutional conditions of the bottom.

#### AQUATIC INSECTS

Aquatic insects are doubtless abundant during spring and early summer in the lower parts of Salt Fork and in the Big Vermilion River. A few species were collected incidentally at some of the molluscan stations. These are listed in Table I, in the order of their occurrence in the stream.



It will be noted that the nymph and larval forms of most species appear coincident with the degree of sewage pollution. Chironomus and Libellula are, seemingly, able to accommodate themselves to the contaminated or polluted condition of the water in the neighborhood of St. Joseph. The adult beetles, breathers of free air, are not affected directly by these unfavorable conditions and occur in great abundance, even in the heavily polluted parts of Salt Fork above St. Joseph. The Ephemeroidea occur for the most part far down the stream where the water is at most only contaminated. The Neuroptera and Plecoptera are clean water forms and were found only in the Middle Fork which does not carry sewage. These are also to be found, probably, in the Big Vermilion below Middle Fork, but no attempt was made to discover these animals when that part of the stream was examined.

TABLE I. DISTRIBUTION OF INSECTS

	Old River bed	St. Joseph	Bridge below St. Joseph	Bench mark 655	Mile above iron bridge near Sidney	Iron bridge	Middle Fork
Diptera							
<i>Chironomus decorus</i> Joh., larva.....	x	x	x		x		
Odonata							
<i>Libellula pulchella</i> Drury, nymph.....	x	x					
Coleoptera							
<i>Gyrinus analis</i> Say, adult.....		x					
<i>Dineutes assimilis</i> Aubé, adult.....		x					
<i>Cnemidotus 12-punctatus</i> Say, adult.....		x	x				
<i>Laccophilus maculosus</i> Say, adult.....		x					
<i>Copelatus glyphicus</i> Say, adult.....		x					
Hemiptera							
<i>Corixa</i> , nymph.....			x			x	
Diptera							
<i>Cricolopus trifasciatus</i> F., larva (?).....			x				
Ephemeroidea							
<i>Hexagenia bilineata</i> Say, nymph.....				x			
<i>Heptagenia</i> , nymph.....					x		
<i>Trichoptera</i> , larva.....						x	
Odonata							
<i>Ophiogomphus</i> , nymph.....							x
Neuroptera							
<i>Corydalus</i> , larva.....							x
Plecoptera							
<i>Perla</i> , nymph.....							x



## HIGHER VERTEBRATES

Vertebrates characteristic of aquatic environments were fairly common in most parts of the Big Vermilion River valley. Three species of turtles were observed: the western painted terrapin (*Chrysemys cinerea* Bonnat-terre), the snapping turtle (*Chelydra serpentina* Linn.) and the soft shelled turtle (*Platypeltis spinifera* LeSueur). The garter snake (*Thamnophis sirtalis* Linn.) was observed swimming across the stream in several places. The fox snake (*Elaphe vulpinus* Baird and Girard) was seen on several occasions near the margin of Salt Fork above St. Joseph. Frogs, among which the pickerel frog (*Rana palustris* LeConte) was noted, were abundant in many places, and tadpoles of all ages were abundant in both the Big Vermilion and Sangamon rivers.

Aquatic birds were occasionally seen in both river valleys. The little green heron (*Ardea virescens* Linn.) and the great blue heron (*Ardea herodias* Linn.), as well as the American bittern (*Botaurus lentiginosus* Montague) were seen repeatedly, especially in the old river cut-offs between Urbana and St. Joseph. Where high banks occur the kingfisher (*Ceryle alcyon* Linn.) made the woods resound with its rattle-like notes. These birds feed largely on young fish and in this way affect the mussel distribution by reducing the number of fish that may bear glochidia. Shore birds, among which were noted Wilson's snipe (*Gallinago delicata* Ord.), solitary sandpiper (*Helodromus solitarius* Wilson), yellowlegs (Totanus), sora rail (*Porzana carolina* Linn.), and killdeer (*Oryzopsis vociferus* Linn.). The pied-billed grebe (*Podilymbus podiceps* Linn.) is seen frequently during spring and autumn on Crystal Lake and in the more pond-like reaches of the Salt Fork. Many of the shore birds feed on mollusks and insects which they find along the shores of the Big Vermilion River system. During migrations, the river valley and its tributaries are fairly alive with birds of all kinds, and at such times the region is well adapted for bird study.

The presence of the muskrat (*Ondatra zibethica* Linn.) is attested by the number of piles of opened mussel shells, the animals of which have provided this mammal with many a meal. In these muskrat piles have been found the shells of many species that are rare or difficult to find alive in the streams.

The abundance of all groups of animal life in the Big Vermilion system indicates that it is a favorable environment for an optimum biota. With the exception of the upper twenty miles more or less seriously affected by sewage pollution, the stream is one of the best collecting grounds in the State, a condition indicated by the very large mussel fauna of thirty-eight species and races, recorded in the following pages.

## FISH FAUNA OF THE BIG VERMILION RIVER

The close relationship between the mussel fauna and the fish fauna, through the breeding habits of the former, render a knowledge of the fish

fauna of the Big Vermilion necessary. As a large mussel fauna lives in the stream it follows as a corollary that there must also be a fish fauna of comparable size. Fortunately, Dr. S. A. Forbes, caused extensive collections to be made in 1901, and these are listed on the maps accompanying the work on the Fishes of Illinois, by Forbes and Richardson (1908). Fifty species are recorded from the Big Vermilion River and its tributaries (see Table II). It will be seen that at this date 28 species were found below Urbana, in that portion of the stream now heavily polluted.

Between the years 1908 and 1912, the Salt Fork between Urbana and St. Joseph was deepened and straightened and the bottom fauna was completely destroyed. In the canal thus formed, for the purpose of carrying off the sewage of the Twin-Cities, no living clams, crayfish, or other clean water animals have been found, and but one school of young fish (bullheads) was observed during several examinations of this part of the stream. It is possible that during periods of high water in the spring, some hardy fish may venture into this heavily polluted area. Below St. Joseph it is quite probable that some fish are found during high water periods. A few minnows were observed near the station called bench mark 655, about fifteen miles below Urbana. A farm boy reported that bullheads could be caught at high water on set lines.

Below bench mark 655, and for some distance above it, fish must resort in some numbers because of the presence of a fair sized mussel fauna (see Table III). Young mussels, however, were not seen in any number above the Homer Park dam, and it is possible that the upper stream is now little visited by fish suitable for glochidial infection. Below the dam, young mussels are plentiful at all points examined.

Information concerning the species of fish that carry glochidia of the river mussels is still of a fragmentary character. Suber (1912), Howard (1914), and other workers of the U. S. Bureau of Fisheries have published considerable data on this subject, but much more is needed before one can fully understand the relation between mussels and fish.

Three species of mussels living in Salt Fork and other parts of the Big Vermilion River are known to have glochidia encysted on five species of fish, all of which have been reported from the Big Vermilion, viz.:

Mussels	Fish
<i>Lampsilis anodontoides</i>	<i>Lepomis humilis</i>
" <i>anodontoides</i>	<i>Pomoxis sparoides</i>
" <i>anodontoides</i>	" <i>annularis</i>
<i>Quadrula metanevra</i>	<i>Lepomis pallidus</i>
" <i>pustulosa</i>	<i>Pomoxis annularis</i>
" <i>pustulosa</i>	<i>Ictalurus punctatus</i>

The abundance of desirable species of mussels in the Big Vermilion indicates that it may serve as a reservoir for button material, the species being easily transported to laboratories anywhere in the state for artificial infection of fish.

TABLE II. DISTRIBUTION OF THE FISH FAUNA IN THE BIG VERMILION

	Above Urbana	Below Urbana	Spoon River	Below Spoon River	Near Sidney	Salt Fork Junction	Middle Fork	Danville	North Fork
<i>Carpiodes difformis</i> Cope. Blunt-nosed silver carp. ....	x				x	x	x	x	
<i>Carpiodes velifer</i> (Raf.). Quillback; Silver carp. ....			x	x	x		x		
<i>Erimyzon sucetta oblongus</i> (Mitchill). Chub-sucker. ....	x	x	x	x	x		x	x	
<i>Minytrema melanops</i> (Raf.). Spotted Sucker. ....	x	x	x	x	x		x		
<i>Catostomus commersonii</i> (Lac.). Common Sucker. ....	x	x	x	x	x	x	x		
<i>Catostomus nigricans</i> (Le Sueur). Hog sucker. ....					x	x	x	x	
<i>Moxostoma aureolum</i> (LeSueur). Common red-horse. ....	x			x	x	x	x	x	
<i>Moxostoma breviceps</i> (Cope). Short-headed red-horse. ....		x							
<i>Camptostoma anomalum</i> (Raf.). Stone-roller. ....	x	x	x	x	x	x	x	x	x
<i>Hybognathus nuchalis</i> Agassiz. Silvery minnow. ....			x				x		
<i>Pimephales notatus</i> (Raf.). Blunt-nosed minnow. ....	x	x	x	x	x	x	x	x	
<i>Semotilus atromaculatus</i> (Mitchill). Horned-dace. ....				x			x	x	
<i>Abramis crysoleucas</i> (Mitchill). Golden shiner. ....	x	x	x	x	x		x		
<i>Cliola vigilax</i> (B. & G.). Bullhead minnow. ....						x	x	x	
<i>Notropis cayuga</i> Meek. Cayuga minnow. ....				x					x
<i>Notropis blennioides</i> (Girard). Straw-colored minnow. ....	x	x	x	x	x	x	x	x	x
<i>Notropis illecebrosus</i> (Girard). Minnow. ....							x	x	x
<i>Notropis whippelii</i> (Girard). Steel-colored minnow. ....	x	x	x	x	x	x	x	x	x
<i>Notropis cornutus</i> (Mitchill). Common shiner. ....		x				x	x	x	x
<i>Notropis atherinoides</i> Raf. Shiner. ....				x	x	x	x	x	
<i>Notropis umbratilis atripes</i> (Jordan). Blackfin. ....			x		x	x	x		x
<i>Ericymba buccata</i> Cope. Silver-mouthed minnow. ....	x	x	x	x	x	x	x	x	x
<i>Phenacobius mirabilis</i> (Girard). Sucker-mouthed minnow. ....	x	x	x	x	x	x	x	x	x
<i>Hybopsis amblops</i> (Raf.). Big-eyed chub. ....				x	x	x	x	x	x
<i>Hybopsis storerianus</i> (Kirtland). Storer's chub. ....							x		
<i>Hybopsis kentuckiensis</i> (Raf.). River chub. ....							x	x	x
<i>Ictalurus punctatus</i> (Raf.). Channel-cat. ....				x		x	x	x	
<i>Ameiurus natalis</i> (LeSueur). Yellow bullhead. ....	x		x						x
<i>Ameiurus melas</i> (Raf.). Black bullhead. ....	x	x	x	x			x		x
<i>Noturus flavus</i> Raf. Stonecat. ....							x		x
<i>Schilbeodes gyrinus</i> (Mitchill). Tadpole cat. ....	x	x	x	x	x		x		x
<i>Schilbeodes murus</i> (Jordan). Brindled stonecat. ....				x	x	x	x	x	x
<i>Esox vermicularis</i> Le Sueur. Little pickerel. ....	x	x		x			x		x
<i>Fundulus notatus</i> (Raf.). Top minnow. ....	x	x	x	x	x		x		x
<i>Labidesthes sicculus</i> (Cope). Brook silversides. ....	x	x		x	x	x	x		

TABLE II—(continued)

	Above Urbana	Below Urbana	Spoon River	Below Spoon River	Near Sidney	Salt Fork Junction	Middle Fork	Danville	North Fork
<i>Pomoxis annularis</i> Raf. White crappie. ....	x								
<i>Pomoxis sparoides</i> (Lacepede). Black crappie. ....	x	x	x	x				x	
<i>Lepomis megalotis</i> (Raf.). Long-eared sunfish. ....	x	x	x	x	x	x	x	x	x
<i>Lepomis humilis</i> (Girard). Orange-spotted sunfish. ....		x	x	x	x	x	x	x	x
<i>Lepomis pallidus</i> (Mitchill). Blue gill. ....				x					
<i>Micropterus dolomieu</i> Lacepede. Small-mouthed black bass. ....					x	x			
<i>Micropterus salmoides</i> (Lac.). Large-mouthed black bass. ....	x		x	x	x			x	
<i>Percina caprodes</i> (Raf.). Log-perch. ....		x	x					x	x
<i>Hadropterus phoxocephalus</i> (Nelson). ....		x							
<i>Hadropterus aspro</i> (C. & J.). Black-sided darter. ....	x	x	x	x	x	x	x	x	x
<i>Diplesion blennoides</i> (Raf.). Green-sided darter. ....		x	x	x	x	x		x	x
<i>Boleosoma nigrum</i> (Raf.). Johnny darter. ....	x	x	x	x	x	x	x		x
<i>Etheostoma jessiae</i> (Jordan & Brayton). ....				x					x
<i>Etheostoma coeruleum</i> Storer. Rainbow darter. ....		x	x		x	x	x	x	x
<i>Etheostoma flabellare</i> Raf. Fan-tailed darter. ....		x	x			x		x	x
Total species from each station. ....	19	34	42	28	30	27	21	27	26



TABLE III. DISTRIBUTION OF THE UNIONIDAE IN THE BIG VERMILION RIVER

SYMBOLS a, abundant c, common f, infrequent l, living D, dead g, gravel m, mud s, sand	Upper Salt Fork	Drainage ditch	Old stream bed	Crystal Lake	Salt Fork, bridge 1	Salt Fork, bridge 2	Salt Fork, bridge 4	Salt Fork, bridge 7	Salt Fork, bridge 9	Spoon River, 1 mile	Spoon River, 2 miles	St. Joseph	Bridge below St. Joseph	Natural dam	Big bend	Below big bend	Bench mark 655	Mile north of iron bridge	Iron bridge, N. of Sidney	Cement bridge, E. of Sidney	Railroad bridge, E. of Sidney	4 miles above Homer dam	3½ miles above Homer dam	2 miles above Homer dam	Below Homer dam	Below Homer dam	South of Muncie	Stony Creek	Salt Fork junction	Middle Fork	Big Vermillion River	Near Danville
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
Stats on number . . . . .	18	12	15	36	12	10	15	12	12	18	18	18	20	18	18	20	16	18	18	20	16	15	12	15	20	15	10	10	12	10	31	
Character of bottom . . . . .	m	m	lm	c	sg	eg	ss	ss	sg	m	m	m	m	m	m	m	m	s	s	s	s	gs	gs	gs	sg	sg	sm	ss	as	gm		
Depth of water (inches) . . . . .	18	12	15	36	12	10	15	12	12	18	18	18	20	18	18	20	16	18	18	20	16	15	12	15	20	15	10	10	12	10		
<i>Carunculina parva</i> . . . . .	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD	LD		
<i>Unioemerus tetralamus</i> . . . . .	c.	f	c	c	sg	eg	ss	ss	sg	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i		
<i>Anodonta grandis</i> . . . . .	c	c	c	c	sg	eg	ss	ss	sg	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i		
<i>Anadonia grandis</i> . . . . .																																
<i>Anadonia complanata</i> . . . . .																																
<i>Fusconota rubiginosa</i> . . . . .																																
<i>Ambledia undulata</i> . . . . .																																
<i>Quadrula pustulosa</i> . . . . .																																
<i>Coreculina glauca</i> . . . . .																																
<i>Strophitus edentulus pavonius</i> . . . . .																																
<i>Amphidromia elegans</i> . . . . .																																
<i>Lasmigona costalis</i> . . . . .																																
<i>Alasmidonta marginata</i> . . . . .																																
<i>Pleurostoma coccineum</i> . . . . .																																
<i>Lampetis ventricosa</i> . . . . .																																
<i>Anodonta imbecilis</i> . . . . .																																
<i>Lasmigona compressa</i> . . . . .																																
<i>Lampetis anomala</i> . . . . .																																
<i>Lampetis multiradiata</i> . . . . .																																
<i>Admonatus elliptiformis</i> . . . . .																																
<i>Admonatus ligamentina</i> . . . . .																																
<i>Quadrula lachrymosa</i> . . . . .																																
<i>Quadrula metanera</i> . . . . .																																
<i>Quadrula metanera wardii</i> . . . . .																																
<i>Rotundaria tuberculata</i> . . . . .																																
<i>Tritogonia tuberculata</i> . . . . .																																
<i>Obovaria circulus</i> . . . . .																																
<i>Pleurobema clava</i> . . . . .																																
<i>Anodonta buchanensis</i> . . . . .																																
<i>Quadrula cylindrica</i> . . . . .																																
<i>Euryina sris</i> . . . . .																																
<i>Truncilla perplexa rangiana</i> . . . . .																																
Total species . . . . .	3.	1	3	6.						11	5	2.	6.	2	16	15	6	8	8	4	5	9	1	11	3	28	0	17	0	20	3	
Distance in miles from Urbana . . . . .	5	10	10	3	1½	2½	4	6½	8	10	10	10	12	14	14½	14½	15½	16½	17½	19½	20	22½	23¾	24¾	27	27	36	36	44	45	46	
Hours given to collecting . . . . .					5	5	5	5	5	3	4	6	3	4	1	1	5	3	1	2	2	3	2	2	6	1	2	1	3	4	4	

TABLE IV. DISTRIBUTION OF SPHAERIDAE, GASTROPODS, AND ASSOCIATED ANIMALS IN THE BIG VERMILION RIVER

[illegible]

## GENERAL DISTRIBUTION OF THE MOLLUSK FAUNA

It will be noted in Table III that the mussels were found in greatest abundance in a bottom composed of sand or gravel, or both, and were fewer in number of species, as well as in individuals, on a mud bottom. As a rule the mussels were found in abundance on the shallow riffles and were often absent from the deeper places in which the bottom was composed of soft mud. A notable exception to this rule occurs at Homer Park where the largest mussel fauna is found in a mud bottom, and where this kind of a bottom produced eleven more species (28) than did the sand and gravel riffles a short distance below (17). This station has been used by Professor Frank Smith for many years as a field habitat for his zoology classes and the mussel fauna is, therefore, better known than that of any other locality on the stream. Although visited several times a year for nearly a score of years, there seems no diminution of the fauna in either species or individuals. A day spent at this station, during which two collectors examined the stream, yielded 24 of the 28 species. This indicates the great abundance of the fauna, which may be due in large measure to the aerating influence of the dam situated just above the collecting grounds.

The stream below the dam at Homer Park is an excellent place in which to study the ecological conditions governing the distribution of the mollusk fauna in a small stream. There is first a very shallow stream below the dam (Fig. 14) flowing over gravel and boulders, in which a few gastropods and small bivalves (*Sphaerium*) live in considerable abundance (Fig. 15). Mussels are rare. Then follows a comparatively deep area of the stream (2-3 feet) flowing over a bed of fine sand or mud in which mussels are abundant and gastropods rare (Fig. 13). This is followed by a moderately shallow stretch of the stream (1-2 feet) which flows over a bottom of coarse sand and gravel in which mussels are found in abundance, although not as numerous in species, as in the mud habitat. A few gastropods live here. These conditions are exceptional in Salt Fork and are not duplicated in any other part of the stream above Danville.

Some species of mussels, as *Anodonta*, *Anodontoides*, and *Unio*, prefer a mud bottom and thrive only in such situations, but the great majority of the naiades prefer a sand or gravel bottom in water with considerable current, and this is the reason they are so abundant in the riffles of all streams. Among the smaller bivalves (*Sphaerium* and *Pisidium*), the majority of species prefer a mud or fine sand habitat. Of the snails or gastropods, *Pleurocera* and *Goniobasis* are usually found in a



rocky (gravel) habitat while *Campeloma* prefers a mud or fine sand bottom. *Physa* lives in both mud and on rocks and *Ancylus* on vegetation or in empty shells of mussels. The ecological preferences of these species, as well as the associated animals, are shown in Table IV.

#### ECOLOGICAL VARIATION

The 35 species and varieties of Unionidae found in the Big Vermilion River west of Danville show an interesting distribution. Table III clearly indicates that there is a more or less gradual increase in the number of species as the stream increases in size. Taking into consideration both dead and living naiads and ignoring for the time the effect of sewage pollution on the distribution, the increase in species correlated with the increase in distance in miles from Urbana may be expressed in the following table:

TABLE NUMBER V. INCREASE IN SPECIES WITH DISTANCE

<i>Station</i>	<i>No. of Species</i>	<i>Distance from Urbana</i>
Big bend.....	6	14.25 miles
One mile north iron bridge.....	12	16.50 "
Railroad bridge.....	15	20.00 "
Two miles above Homer dam.....	14	24.75 "
Homer Park.....	28	27.00 "
South of Muncie.....	23	36.00 "
Salt Fork junction.....	15	44.00 "
Middle Fork.....	22	45.00 "
Big Vermilion.....	21	46.00 "

The sudden rise in number of species at Homer Park is noteworthy and is due to the exceptionally favorable environment, good depth of water, favorable bottom, plenty of food, and a fully normal supply of dissolved oxygen provided by the dam just above the Park. The dam appears to be an effective barrier to the migration of mussels, and it would also seem difficult for fish to pass the dam, except at very high water, and thus migration in the glochidial stage is rendered difficult or impossible. In the table it may be noted that 17 species occur at five stations, two to eight miles above the dam and 28 species occur below the dam. Seventeen species are common to both areas and 12 species are found below but not above the dam. This distribution is shown in Table VI.

A striking feature of naiad distribution, noted repeatedly in several species, is the conspicuous change in the shape of the shell as the distance from the headwaters of the stream increases. Species that normally have swollen or globose shells in the larger rivers, occur as flat or compressed forms in the headwaters of these streams. An increase in length of shell as correlated with decreased obesity is also noted, and also, a decrease in tuberosity. Ortmann (1920) has recently ably discussed this matter and shows that the rule holds good for many species in widely separated areas; the writer cannot fully agree with Ortmann in reducing so many species



of Naiades to varieties on the basis of compression in the headwaters of streams. The same species varies in obesity, but it is the same species, whether thin or fat. Other characters are usually present which separate the allied species.

TABLE VI. SPECIES OF UNIONIDAE FOUND ABOVE AND BELOW HOMER PARK DAM

Both Above and Below Dam	Below Dam Only
<i>parva</i>	<i>anodontoides</i>
<i>ferussacianus</i>	<i>ellipsiformis</i>
<i>grandis</i>	<i>ligamentina</i>
<i>imbecillis</i>	<i>multiradiata</i>
<i>edentulus</i>	<i>lachrymosa</i>
<i>pavonius</i>	<i>metanevra</i>
<i>luteola</i>	<i>wardii</i>
<i>lienosa</i>	<i>R. tuberculata</i>
<i>complanata</i>	<i>T. tuberculata</i>
<i>rubiginosa</i>	<i>circulus</i>
<i>undulata</i>	<i>clava</i>
<i>pustulosa</i>	<i>glans</i>
<i>costata</i>	
<i>marginata</i>	
<i>coccineum</i>	
<i>ventricosa</i>	
<i>compressa</i>	

In the Big Vermilion this variation in compression is marked in several species. Thus *Rotundaria tuberculata*, *Pleurobema coccineum*, and *Amblema* are more compressed than are individuals from the Wabash River below the junction of the Big Vermilion with that river. *Quadrula pustulosa* is smaller than the same species lower down in the Salt Fork, and the same may be said of *Alasmidonta marginata* and *Strophitus edentulus*. That the rule does not always hold good is shown by the variation of *Fusconia rubiginosa* which is abundant in most parts of the Big Vermilion and its tributaries. Measurements are given in Table VII, showing the length and breadth of several species in different parts of the Salt Fork from below Urbana to the Big Vermilion. The percentage of width to length is also shown.

It will be seen that the average index for the first lot is 42 per cent and for the last lot, 46 miles down stream, is almost the same, 45 per cent. These averages compare well with some of those given by Ortmann (1920: 283). It was observed, however, that in the Salt Fork and Big Vermilion the obese individuals occurred with the compressed specimens the former increasing in ratios as the distance down stream increased. The variety *wardii* of *Quadrula metanevra* occurred in two places in Salt Fork but always in company with the typical form. In the cases cited above ecological features cannot be called into account in locating the cause of the com-

pression of the shell, for all live in the same section of the stream under identical conditions. The rule cited by Ortmann, however, seems to be applicable in most cases.

Several species increase in size toward the lower part of the river. This is especially true of *Anodonta grandis*, *Strophitus edentulus*, *Alasmidonta marginata*, *Eurynia lienosa*, *Lampsilis luteola*, *Amblema undulata*, and *Lampsilis ventricosa*. A few others show some increase at different stations. One species, *Unio merus tetralasmus*, is apparently confined to the upper, smaller tributary streams of Salt Fork. It was common in the ditch north of Urbana; in Crystal Lake, Urbana, in Spoon River; and at Muncie in a small tributary. Two broken valves were found at the station called the natural dam, but these are believed to have been washed into this stream from a nearby tributary which was dry when this part of the Salt Fork was examined (September 25). *Tetralasmus* probably also occurs in the

TABLE VII. VARIATION OF *Fusconaia Rubiginosa*

Length	Width	Per cent	Station No.	Distance from Urbana
58	23	39	17	15¼ miles
62	26	42	..	.....
61	31	50	..	.....
68	27	39	..	.....
79	33	42	..	.....
86	33	38	24	24¾ miles
89	41	46	..	.....
90	31	34	25	27 miles
82	35	42	..	.....
89	47	52	..	.....
71	30	42	26	36 miles
67	30	44	..	.....
102	41	40	30	46 miles
65	30	46	..	.....
86	43	50	..	.....

upper part of Middle Fork and in North Fork, but the upper parts of these streams have not been examined. The majority of the other species occur at several stations along the Salt Fork and its tributaries and no particular variation in distribution was observed except as already noted.

Three mussel species and varieties were found in Crystal Lake that are exotic as far as the Big Vermilion River is concerned. These are *Anodonta grandis gigantea*, *Anodonta corpulenta*, and *Unio merus tetralasmus sayii*. These species were artificially introduced into this body of water about 1908 by a member of the zoological department of the University of Illinois. They originally came from a stream in western Indiana. That these mussels found a favorable environment and have thrived during these years is evidenced by the number of fine specimens recently collected when the lake was partly drained. Only the *Unio merus* was rare, but one specimen being found. As Crystal Lake is not connected with the Salt Fork

stream, these species have not been able to enter the Big Vermilion drainage.

As has been noted in the Illinois River (Forbes and Richardson, 1919), the mussel fauna gradually increases as the distance from the source of sewage pollution becomes greater. In the Salt Fork the fauna becomes normal at about 20 miles from the source of pollution at Urbana. In the Illinois River a normal fauna is not found within 80 miles (Hennepin) of the source of pollution indicating that the quantity of sewage is so great that the river must flow this distance before purifying itself sufficiently for the residence of normal aquatic life. That a normal fauna should be found within 20 miles of the source of pollution in the Salt Fork, though a much smaller stream carrying a smaller amount of sewage, is quite surprising when it is remembered that no large tributaries enter the stream above Spoon River, and indicates that self purification is active. The shallowness of the water (less than a foot on the average in fall and winter) probably provides a larger quantity of dissolved oxygen than would be possible in waters of a deeper stream. It was especially noted that *Amblema undulata* and *Lasmigona complanata*, of the larger species, withstood the absence of water better than any of the other comparable species. These mussels also resisted polluted conditions better than others and this fact is important in connection with mussel propagation for button shells.

#### COMPARISONS WITH OTHER RIVER SYSTEMS

It is of interest and value to compare the mussel fauna of the Big Vermilion River with that of some other rivers of comparable size and development. The United States Bureau of Fisheries has conducted mussel investigations of several of the rivers of Illinois and adjacent states and one of these, the Kankakee (Wilson and Clark, 1912), may well be compared with the Big Vermilion. The mussel fauna of the Sangamon River is also included, the data given being gathered from several sources, but principally from personal collections and from collections in the Museum of Natural History of the University of Illinois. Some species not listed by Wilson and Clark are included from Baker's Catalog of Illinois Mollusca (1906). These are indicated by an asterisk.

TABLE VIII. DISTRIBUTION OF UNIONIDAE IN THREE RIVER SYSTEMS

Length of river in miles. ....	Vermilion 90	Kankakee 300	Sangamon 150
<i>Quadrula cylindrica</i> .....	x		
" <i>metanevra</i> .....	x	x	x
" <i>metanevra wardii</i> .....	x		x
" <i>pustulosa</i> .....	x	x	x
" <i>lachrymosa</i> .....	x	x	x
" <i>ebena</i> .....		x	x
<i>Trilogonia tuberculata</i> .....	x	*	x
<i>Amblema undulata</i> .....	x	x	x
" <i>peruvians (plicata)</i> .....		*	

TABLE VIII—(continued)

	Vermilion	Kankakee	Sangamon
<i>Fusconaia rubiginosa</i> .....	x	x	x
“ <i>trigona</i> .....		x	
“ <i>solida</i> .....		*	
<i>Rotundaria tuberculata</i> .....	x	x	
<i>Pleurobema clava</i> .....	x	x	
“ <i>coccineum</i> .....	x	x	x
<i>Plethobasus aescopus</i> .....		x	
<i>Elliptio gibbosus</i> .....		x	x
<i>Unio merus tetralasmus</i> .....	x		
“ <i>tetralasmus sayii</i> .....	x		
<i>Strophitus edentulus</i> .....	x	x	x
“ <i>edentulus pavonius</i> .....	x		x
<i>Anodonta grandis</i> .....	x	x	x
“ <i>grandis gigantea</i> .....	x		
“ <i>corpulenta</i> .....	x		
“ <i>imbecillis</i> .....	x	x	
<i>Anodontoides ferussacianus</i> .....	x		x
“ <i>f. buchanensis</i> .....	x	x	
<i>Arcidens confragosus</i> .....			x
<i>Lasmigona compressa</i> .....	x	x	
“ <i>costata</i> .....	x	x	x
“ <i>complanata</i> .....	x	x	x
<i>Alasmidonta marginata</i> .....	x	x	x
“ <i>calceola</i> .....		x	x
<i>Ptychobranchius phaseolus</i> .....		x	
<i>Obliquaria reflexa</i> .....		*	
<i>Plagiola securis</i> .....		*	
<i>Amygdalonaia elegans</i> .....	x	*	
“ <i>donaciformis</i> .....		■	
<i>Proptera alata</i> .....		x	
<i>Paraptera gracilis</i> .....		*	
<i>Obovaria circulus</i> .....	x		
“ <i>ellipsis</i> .....		x	
<i>Actinonaias ligamentina</i> .....	x	x	x
“ <i>ligamentina nigrescens</i> .....		x	
“ <i>ellipsiformis</i> .....	x	x	x
<i>Carunculina parva</i> .....	x	x	x
“ <i>glans</i> .....	x	*	
<i>Eurynia recta</i> .....		x	
“ <i>subrostrata</i> .....		x	
“ <i>iris</i> .....	x	x	
“ <i>fabalis</i> .....		x	
“ <i>lienosa</i> .....	x	x	
<i>Lampsilis fallaciosa</i> .....		x	
“ <i>anodontoides</i> .....	x		
“ <i>ventricosa</i> .....	x	x	x
“ <i>multiradiata</i> .....	x	x	
“ <i>capax</i> .....			x
“ <i>luteola</i> .....	x	x	x
“ <i>higginsii</i> .....		*	
<i>Truncilla sulcata</i> .....		x	
“ <i>perplexa rangiana</i> .....	x		
Total species in each river.....	38	48	25



It is noteworthy that with a length of 300 miles and with two tributaries of large size (Iroquois River, 100 miles in length, Yellow River, 65 miles long) the Kankakee River has a mussel fauna only 21 per cent greater than the Big Vermilion River with a length of 90 miles and no very long tributaries. Other species will probably be found in the Big Vermilion below Danville, which was not examined during this survey, and these may bring the total nearer to that of the Kankakee River. The Sangamon River undoubtedly contains many more species than listed in the table, and these will be found when additional collecting is carried on. The table shows that the mussel fauna of the Big Vermilion River is of large size as compared with other streams of similar character.

## SYSTEMATIC DISCUSSION OF THE MOLLUSCA

In this chapter the species of mollusks, both Pelecypoda (mussels, clams) and Gastropoda (snails), are discussed in relation to their distribution in the Big Vermilion River, special emphasis being given the Unionidae or river mussels on account of their economic importance. The influence of sewage pollution of the stream on the mollusk fauna is also referred to. The species collected in the Sangamon River at Mahomet and elsewhere are included for purposes of comparison.

The classification followed for the Unionidae is that proposed by Simpson (1900, 1914) and extended by Ortmann (1912, 1918). The sequence of groups is that set forth in Walker's Synopsis recently published (1918). It will be noted that the newer classification necessitates the adoption of several new names, both generic and specific, but these seem, on the whole, justified by the rules of nomenclature and are a natural result of the advancement of knowledge on the subject.

For the purpose of providing reliable data on the particular characteristics of the mussels and other mollusks in this stream for comparison with similar features of this group of animals in other streams, a feature almost totally lacking in the literature, considerable space is devoted to descriptions of the minor variations and pathological conditions of each species in different environments. This has been done, more or less extensively, in several reports on the mussel faunas of three or four of our Illinois, Indiana, and other streams (Wilson and Clark, Danglade). It will be noted that there are certain features characteristic of the species in one stream not shared by the same species in other streams, as, for example, *Lampsilis ventricosa* which differs markedly in coloration and even in shape in the two river systems herein considered. Similar data on our other rivers would provide a body of facts of considerable importance.

### FAMILY UNIONIDAE

#### 1. *Quadrula* (*Quadrula*) *cylindrica* (Say). Rabbits-Foot.

This species was not found in the Salt Fork above a point about a mile west of its junction with the Middle Fork, 44 miles from Urbana. As it is not listed from the neighborhood of Muncie its westward extension in the stream lies somewhere between Muncie and Middle Fork. Even in this part of the river it is rare and the specimens obtained are small, of dark color and resemble the form called *strigillatus* by Wright. *Cylindrica* is not a widely distributed species in Illinois, if one may judge by the records at hand. Danglade (1914) did not find it in the Illinois River

nor is it listed by other students. It has been reported by several conchologists from the Wabash River (Baker, 1906:79) and the Ohio River, in which streams it is common and of large size and fine color. The species probably would not thrive in polluted water. It was not found in the Sangamon River at the places visited. Owing to its peculiar shape it is not adapted for the cutting of button blanks and is considered worthless by the mussel fishermen.

## 2. *Quadrula (Quadrula) metanevra* Rafinesque. Monkey-Face.

This naiad is apparently a rare species in Salt Fork occurring sparingly from Homer Park to Middle Fork. It begins to increase in number of individuals near the Middle Fork, where the specimens are also larger and more brilliantly colored. All but one of the specimens collected are typical in form and coloring. Individuals from the Big Vermilion below Middle Fork are larger than those collected above this point. The species is also more abundant. It is found on both a mud and a gravel-sand bottom. Specimens from Homer Park are darker and less conspicuously rayed than those from Middle Fork, and are also less pustulose. *Metanevra* is rare in the Sangamon River, living on both a sand and gravel bottom.

### 2a. *Quadrula (Quadrula) metanevra wardii* (Lea).

Two specimens referable to this variety have been collected from the Big Vermilion; one near Muncie, in the Salt Fork, and one in the Middle Fork, above its entrance into the Vermilion River. These individuals are more elongated and compressed than the typical form and the tubercles are not as heavy, in fact are reduced to large pustules. Professor Smith has found the variety more common in the Sangamon River than the typical form, and until these two specimens were found in the Big Vermilion drainage, *wardii* was supposed to be the predominant form in the Sangamon while the typical form was believed to be the only form of this species found in the Big Vermilion, at least above Danville. *Wardii* is, as far as present material indicates, very rare in the Salt Fork and other tributaries of the Big Vermilion.

## 3. *Quadrula (Theliderma) pustulosa* (Lea). Warty-Back; Pimple-Back.

This is the most abundant *Quadrula* in both the Salt Fork and the Sangamon River, rivalling in number any other mussel species in the lower part of the Salt Fork. It does not occur in any abundance above the Homer Park dam, but below this point it is common, of large size, fine color, and good nacre. The sewage pollution has evidently affected this species as others and, with rare exceptions, only dead shells could be found above the Homer Park dam. Below the dam it occurs commonly and the increase in number of individuals is largely due to the aerating effect of the flow of water over the dam which provides the dissolved oxygen so

necessary to these animals. The young shells (20mm. in length) are almost smooth with a broad dark green ray or stripe extending from the umbones to the ventral margin of the valve. No young shells were found in the stream above Homer Park dam and the species may not be breeding in this part of the stream at the present time.

The *pustulosa* from Salt Fork exhibit some variation in the pustulosity of the surface, but all are referable to typical *pustulosa*. A few specimens from Homer Park are more quadrate than the average but are otherwise typical. The individuals from the Sangamon River, however, show considerable variation in both form and pustulosity, ranging from nearly circular to quadrate and from almost smooth to quite pustulose. On an average, however, they are less pustulose than the species occurs in Salt Fork. Individuals might be picked out that could be referred to both *dorfeuillianus* Lea and *schoolcraftensis* Lea, but the range of variation is so great that they seem better referred to *pustulosa*. In the Sangamon River *pustulosa* occurs on a sand and gravel bottom but in the Big Vermilion River it is found most abundantly on a mud bottom. The individuals from Homer Park and the Sangamon River, especially the later, are of good size, 70 to 80mm. in length, and the thickness of the shell combined with the clear pearly luster would seem to make them good shells for the button trade. No evidences of parasitism were observed in the shells examined.

#### 4. *Quadrula* (*Theliderma*) *lachrymosa* (Lea). Maple-Leaf.

This handsome shell is very rare in the Salt Fork and was not found at any of the localities in the Sangamon River. In the Salt Fork it has been found only at Homer Park below the dam, and only occasional specimens have been collected here. These are quite typical of the species.

#### 5. *Tritogonia tuberculata* (Barnes). Buck-Horn; Pistol-Grip.

The buck-horn first makes its appearance in Salt Fork at Homer Park below the dam where it is of large size (female 145, male 115 mm.) and fine quality. The shells are densely covered with tear-like pustules which in a few individuals cover the entire surface, though usually confined to the middle and anterior end behind the posterior elevated ridge. Of the specimens collected 40 percent are males. Young specimens 46 mm. in length were found at Homer Park. Individuals from Homer Park are larger than those collected in the Sangamon River, the largest specimens being found on a mud bottom, although it also lives on a sand and gravel bottom. Both the Salt Fork and Sangamon specimens are of good quality from the button makers standpoint.

Abnormalities and pearly growths due to injuries or parasitism are rare in the specimens of this species examined. A few individuals from Homer Park had scattered pin-head pearls and a small patch of discolored



blister formation near the anterior and posterior end, one in each end of two specimens.

**6. *Amblema undulata* (Barnes).** Blue-Point; Three-Ridge.

This characteristic mussel is the most abundant species in the Vermilion River, greatly exceeding (with the possible exception of *Lasmigona complanata*) in number of individuals all other species. It is also able to resist much of the ill effects of sewage pollution and is the first shell met with in the polluted waters of the Salt Fork. Living specimens, however, were not seen above the station called bench mark 655, a distance of over 15 miles from the source of pollution. Empty shells and odd valves occur more or less abundantly from St. Joseph, 10 miles below Urbana, to the station mentioned. As the species lives in fair abundance in the tributary known as Spoon River, for a distance of over two miles up stream from near the mouth of the stream, it is evident that at one time its distribution was equally continuous in the Salt Fork below the junction of Spoon River with Salt Fork, where now there is a break of nearly six miles. This break in the distribution is in all probability due to the sewage pollution, for the stream is admirably adapted by nature as a habitat for this species and has not been disturbed by dredging.

There is great variation in the form of the shell. Many specimens from the upper part of the stream, both Spoon River and Salt Fork as far down as the natural dam, are almost round with a broad 'wing' above the undulations, which may be reduced in number and form (Fig. 34). These shells may be inflated or rather compressed. Other shells are more quadrate and in occasional individuals the umbones are elevated simulating *Amblema peruviana* (*plicata* of authors). These shells have a black or dark brown epidermis in the adult condition. In Spoon River young shells 25 mm. long were common, but few young specimens were found in the Salt Fork above the Homer Park dam. Shells from the lower part of Salt Fork, below Sidney, are as a rule cleaner, the epidermis is of a brighter, lighter brown and are more uniformly quadrate than those from above Sidney. The largest specimen collected measured 140 mm. in length and this seems to be the maximum size for the *undulata* in this stream. Many of this size were seen.

In the Spoon River, and in the upper part of Salt Fork, injured shells are common. The injuries consist of breaks in the shells and subsequent repairs. In one specimen from the upper part of Spoon River, an injury had been received when the mussel was small which resulted in a deep channel across the right valve (Fig. 29) and a ridge, also slightly channelled, on the left valve (Fig. 30). Another shell had nearly a hundred blister pearls on the edge of the posterior margin of the left valve (Fig. 28) and a large blister pearl about midway of the pallial line in the right valve

(Fig. 27). Still another shell had covered a quantity of mud, which had gotten in between the mantle of the animal and the shell, with a thin layer of pearl, forming a large pad-like blister covering the greater part of the interior of the left valve (Fig. 26). The right valve was normal (Fig. 25). These blister pearls, as well as the more valuable free pearls, are believed to be caused by parasites, perhaps distomids. These injured shells are eagerly sought by the pearl hunters and mussel fishermen in the belief that they may contain pearls of value.

The *undulata* from the Sangamon River also exhibit a wide range of variation in the shape of the shell, but not to the degree seen in the material from the Spoon River and Salt Fork of the Big Vermilion River. In the Sangamon, *undulata* is very abundant on a gravel and sand bottom. In the branches of the Big Vermilion it occurs on both a mud and a sand-gravel bottom. As this species is very successful in resisting adverse conditions it is a valuable mussel for propagation in the streams subject to pollution. It is probably not much affected by a moderate amount of sewage in its environment. The button manufacturers consider it a good shell when the undulations are not too heavy to render the cutting of blanks difficult.

#### 7. *Fuscunaia rubiginosa* (Lea). Wabash Pig-Toe.

This mussel is abundant in the lower part of the Salt Fork. It was not found in any abundance above the dam at Homer Park, where it is abundant, and the large number of dead, empty shells observed attest the presence of an unfavorable environment. As it is rare in Spoon River, where some other species are abundant, it is probable that this species requires fairly deep water and a large stream bed to attain good size and abundance in individuals. This characteristic of distribution was also noted by Wilson and Clark (1912:43) in the Kankakee River where *rubiginosa* was found to be more common in the lower part of the river.

There is considerable variation in the form of the shell; some examples are compressed, others quite inflated. Nearly all are distinctly quadrate, but in some examples the ventral margin is convex; in others it is somewhat concave; while in a few it is straight. The individuals from the upper part of the stream, above Homer Park dam, are usually dark brown with a satiny sheen to the epidermis and are almost rayless. Those from the lower part of the river, especially from Middle Fork, are light yellowish brown, quite distinctly rayed. The nacre varies from white to pink or salmon, but is white in the great majority of specimens collected. Young shells 28 mm. in length were common below the Homer Park dam, but were apparently rare above the dam. This may indicate adverse conditions due to sewage pollution and the species may not now be breeding freely, possibly for lack of suitable fish for the glochidia. Young specimens were

also collected in the Big Vermilion River. One of the largest adult individuals found, below Homer Park dam, measured 95 mm. in length; another from the Big Vermilion River measured 103 mm. in length. The species occurs about equally on a mud or sand-gravel bottom.

A single example from Homer Park is worthy of special note. It is large, inflated, almost twice as wide as the average shell of the same size, and is elongate-quadrate in outline. When viewed from within, the valves are basin-shaped. All of the muscle scars are very heavily impressed and the pseudocardinal teeth are much modified and heavier than in normal *rubiginosa*. The lateral teeth are very high, wide and massive. The shell was dead when picked up and badly discolored and notes on the animal, which would have been very desirable, could not be made. The measurements of this shell, together with that of a normal shell of the species, from the same habitat, are given below:

Length, 90; height, 59; width, 50 mm.	Z11163 A, Variety.
“ 82 “ 58 “ 36 mm.	Z11163 B, Normal.

This species also occurs in the Sangamon River, but does not, apparently, attain the dimensions of the Salt Fork specimens, nor does it occur as abundantly. There is but slight variation in form in the Sangamon shells. No pathological specimens were observed in individuals from either river. *Rubiginosa* is not much esteemed by either pearlery or mussel fishermen.

*Rubiginosa* frequently closely resembles *Pleurobema coccineum* in the form of the shell and specimens occur which seem difficult to place satisfactorily. The animals differ in that in *rubiginosa* all four of the gills are used as marsupia while in *coccineum* only the outer gills are so used. As far as the Salt Fork and Sangamon River shells are concerned there has been no difficulty in placing any individual. In this material *rubiginosa* is always quadrate with the umbones large and full, the posterior end of shell is almost sharply truncated and there is a more or less distinct ridge extending from the umbones to the posterior angle of the shell. In *coccineum* the outline is rather ovate, or rounded, there is no posterior ridge and the position of the umbones gives to the shell an oblique appearance which is very characteristic and is absent in *rubiginosa*. The ventral margin in *coccineum* is almost always convex and seldom straight or concave as in *rubiginosa*. The young shell in *coccineum* is also usually more distinctly rayed. The surface of the two species is also different, that of *coccineum* not being 'satiny' as is that of *rubiginosa*. The interior, and even the exterior, of *coccineum* is usually pinkish or salmon colored, although individuals occur with white nacre.



### 8. *Pleurobema clava* (Lamarck). Club-Shell.

This species is rare in most parts of the Big Vermilion examined, and was not found in the Sangamon. It occurs sparingly at Homer Park, abundantly in the Salt Fork near Muncie, and sparingly in the Middle Fork. At Muncie the largest specimen measured 90 mm. in length. The specimens from the Big Vermilion are beautifully marked with broad green rays on young individuals and on the umbonal half of older specimens. Large individuals are almost rayless.

This species has been previously known only from the Wabash River in Illinois (Baker, 1906:77) and the present records, although in the same drainage basin, extend the range of its distribution.

### 9. *Pleurobema coccineum* (Conrad). Thin Niggerhead.

The shell known as *coccineum* attains large size in certain parts of the Salt Fork. It is common, however, only at one place, below the dam at Homer Park. No shells of this species were observed above the station called bench mark 655, which is about 15 miles below Urbana. The shells from habitats above the dam at Homer Park exhibit evidence of an unfavorable environment, the shells having heavy lines of growth which on some specimens are raised to form ridges. These are especially marked at the rest periods (seasonal). The individuals from the upper part of the stream are also more or less pathologic, 50 per cent of the shells being abnormal in form or with pearly growths on the inside of the valves. *Coccineum* is found on both a mud and a sand-gravel bottom.

There is considerable variation in the outline and general shape of the shells from Salt Fork. The outline varies from quadrate to roundly ovate and the ventral margin from nearly straight to strongly convex. Young and half-grown shells seem more uniform than large adult shells. The quadrate individuals may easily be confounded with *Fusconaia rubiginosa*. In the last species, however, the shell is more inflated (*coccineum* is compressed), the umbones are directed upward and not backward, as in *coccineum*, and the posterior portion of the shell has a depressed area and a strong ridge which are absent in *coccineum*. The nacre of *coccineum* is pink of various shades, only two specimens from the Salt Fork having white nacre. In this respect the *coccineum* of the Big Vermilion drainage differ almost constantly from *rubiginosa* which has white nacre. The epidermis in specimens from the upper part of the stream (Homer Park and above) is usually very dark brown with faint evidences of rays. In some specimens, especially from the station three and a half miles above Homer Park dam, the whole shell, inside and outside, is of a delicate pink shade. Individuals from the Middle Fork and the Big Vermilion, where the species is rare, are lighter in color. The two largest specimens collected from the Big Vermilion drainage measure as follows:

Length, 96; height, 75 mm. Quadrate form above Homer dam, Z11114 A.  
" 96 " 80 mm. Rounded form, Homer Park, Z11164 A.



In the Sangamon River *coccineum* is a most abundant and variable mussel, having a smooth, polished shell on which the rays are many and distinct. It also attains a large size, though not as large as specimens from the Big Vermilion drainage. The shape of the shell is more oblique and elliptical than is the species as it occurs in the Big Vermilion and the shell is a trifle more inflated on the average. So marked is the difference that it is comparatively easy to say from the shape of the shell and the surface markings what drainage a particular individual may have come from. The twelve sets of *coccineum* in this collection indicate in a marked degree the fact that species may differ conspicuously in both sculpture and form in different river systems. The nacre of the Sangamon River *coccineum* is more often white than in the Big Vermilion shells. Pearly secretions or pathologic malformations have not been observed in the specimens from the Sangamon River, indicating, without doubt, a more favorable environment than is provided by the waters of the Salt Fork. Young specimens (25–30 mm. long) are more abundant in the Sangamon River than in the Big Vermilion River, and these individuals are beautifully marked with dark green rays on a yellowish or light brown background. Occasional shells are pinkish. The beak markings on the umbones are especially well preserved in these young specimens.

A large right valve from Mahomet is very peculiar. In outline it is ovate, a trifle oblique. The posteroir portion of the valve is much elongated the hinge line is long and straight, and the posterior margin is sharply, obliquely truncated. The umbonal region is near the anterior margin of the valve. The lateral tooth is longer and straighter than in normal *coccineum*. The shell recalls *Pleurobema clava* but is much larger and differently shaped. The valve measures as follows: length 92, height 70 mm.

Ortmann (1918:549) considers *coccineum* a variety or race of *obliquum* (Conrad), together with *solidus* (= *catillus* Conrad), which is also rated as a variety of *obliquum*. To this disposition the writer cannot agree, the forms here listed as varieties being quite as much entitled to specific rank as are many other forms recognized as distinct species which have marked variation and a similar facies. The whole group of *obliquum-solidum-coccineum* are closely related, but I have seen no good reason after examining a large series in the Hinkley and other collections in the Museum collections, for lumping these species as varieties of *obliquum*. As far as Illinois specimens of *obliquum* and *coccineum* are concerned, the two species seem sufficiently distinct for recognition.

#### 10. *Rotundaria tuberculata* Rafinesque. Purple Warty-Back.

This species was found at but two places in Salt Fork, at Homer Park and South of Muncie, and in the Big Vermilion below Middle Fork. At

the first two places it is very rare, only a few individuals having been found by Professor Smith in a number of years. In a days search at Homer Park by two experienced collectors, only two living specimens and odd valves of two others were found. The largest specimen from Homer Park measures 72 mm. in length and 63 mm. in height. This species is one of the most abundant of shells in the Big Vermilion below Middle Fork, where specimens measuring 100 mm. in length are common. The distribution of this species is a good example of the progressive development of a species in the downward course of a stream, for in the course of about twenty miles the size nearly doubles. Beginning as a rare form at Homer Park it becomes one of the most common forms in the Big Vermilion, twenty miles downstream.

All of the Big Vermilion *tuberculata* are of the compressed type, and the shell is covered posteriorly and ventrally with large tear-like pustules. The anterior third of the valve is free from pustulation. The nacre of all shells seen is rich purple, which renders the species valueless for the button makers. *Tuberculata* does not occur in the portions of the Sangamon River examined.

#### 11. *Elliptio gibbosus* (Barnes). Lady-Finger; Spike.

This mussel does not occur in Salt Fork, nor in any tributaries of the Big Vermilion above Danville that have been examined. It is fairly common in the Sangamon River at Mahomet on a sand and gravel bottom. Young and immature shells are distinctly rayed. The nacre of all specimens examined has been purple, no white-nacred individuals being seen. In the Kankakee River white-nacred specimens occur and become the dominant form in the lower part of the stream (Wilson and Clark, 1912:45). In the Illinois River beds of shells occur which have either a white or a purple interior. (Danglade, 1914:42). This familiar shell will probably have to be known as *dilatatus* (Rafinesque) if the original description is definite enough to identify it as the *gibbosus* of Barnes. *Dilatatus* was described in 1820. It is a pity that these names of Rafinesque could not have been applied earlier to these shells and thus saved the confusion which is now resulting from the changes of the old familiar names which zoologists in our universities have used for years in connection with their classes in systematic zoology.

#### 12. *Uniomere tetralasmus* (Say).

This species has been found living only in the upper waters of Salt Fork and in Stony Brook near Muncie. It occurs in fair numbers in the stream above Urbana and in Spoon River. Two broken valves were found in Salt Fork at the station called natural dam about 12 miles below Urbana. No living mussels could be found in the stream at this point and it is believed that the odd valves were washed into Salt Fork from a small

tributary nearby which was dry at the time of our examination. *Tetralasmus* is a species of the small, mud-bottom tributaries and seems not to occur in the larger part of the stream with the larger and heavier mussels. The largest specimen collected measures 55 mm. in length. The colors of the shells are yellow, black, and greenish, the latter in indistinct ray-form.

**12a. *Uniomerus tetralasmus sayi* (Ward).**

Among the *Anodontas* collected in Crystal Lake is a specimen of the shell known as variety *sayi*. It is large for the species but seems otherwise typical. The dimensions are: length, 123; height, 58; breadth, 38 mm. (No. Z 11369). As only *tetralasmus* is found in the Salt Fork and its tributaries it is probable that this form was introduced with the *Anodontas* described on a subsequent page.

**13. *Strophitus edentulus* (Say). Squaw-Foot.**

This mussel once occurred in nearly all parts of the Big Vermilion River but it is now found in any number only below the dam at Homer Park. No living specimens were found above a point four miles above Homer Park dam or 22 miles below Urbana. It occurs, rarely, living, in Spoon River and its absence in a living state for a distance of 12 miles between this tributary and the first habitat in which it was found alive in Salt Fork is striking and suggestive of the harmful effect of sewage pollution. This species reaches its greatest perfection below the dam at Homer Park on a gravel bottom. *Edentulus* also occurs in the Sangamon River, but the individuals from that stream are not as large and are more compressed than the specimens from Salt Fork, which are as a rule quite corpulent. It is also not as abundant in the Sangamon as in the Big Vermilion. Measurements are given below of the largest specimens from the Salt Fork and the Sangamon.

Length, 90; height, 54; width, 41 mm. Salt Fork, Z11174.

" 89 " 57 " 32 mm. Sangamon, Z11227 A.

There is great variation among the shells referred to this species. Typical *edentulus* is rhomboid in form, rather inflated, with prominent, inflated umbones; the posterior margin of the shell is usually sharply, obliquely truncated, and the ventral margin is straight or even slightly convex. The color is usually black without rays. From this type the shell varies to an ovate or elliptical outline, a more or less compressed form, with a rounded, convex ventral margin and with an almost total absence of the strong posterior ridge so characteristic of the usual form. The variation is, as would be expected, toward the variety known as *pavonius*. The shells from Salt Fork are very thick and solid, much more so than in specimens from the Sangamon River. The nacre of the majority of specimens is yellowish in color.



### 13a. *Strophitus edentulus pavonius* (Lea).

This variety is described by Simpson (1914:348) as "Shell generally long elliptical; epidermis yellowish-green, more or less covered with green or brownish-green rays." In its typical form *pavonius* is easily separable from *edentulus*. The variety is almost as common in Salt Fork as is the typical form and there are many intermediate individuals. It is possible, however, to separate all of the *edentulus* from the different stations, 17 lots, into two groups; one with rhomboid or long-ovate outline and with black or brownish, rayless surface; and the other with long-elliptical outline, brownish surface, and many distinct rays. In *pavonius* the height is less as compared with the length than in *edentulus*. These two forms of *Strophitus* were almost always associated together, indicating their close relationship. On the whole *pavonius* is much less variable than typical *edentulus*. Specimens from the Sangamon River at Mahomet are brilliantly rayed with patches of bright green on the ventral margin of the shell.

Wilson and Clark (1912:48) state that the "question of rays appears to be closely related to clearness of water; in turbid streams mussels are usually dull colored, while in clear streams they are usually brightly rayed." This has been our observation in many cases, but the rayed *pavonius* in Salt Fork occurs with the rayless *edentulus* in quiet water on a mud bottom; both also occur in riffles on a sand-gravel bottom.

*Pavonius* is credited by Simpson to Ohio and Indiana; it is probably widely distributed in Illinois, but has most likely been listed under *edentulus* in most cases. It is known from Cook County, Will County, and the Wabash River (Baker, 1906:72). Its presence in the Sangamon River indicates that it is also an inhabitant of the Mississippi River drainage, as well as the Wabash and Ohio drainages. It is quite probable that the distribution of the variety is coincident with that of *edentulus*. The nacre of both *edentulus* and *pavonius* is usually yellowish or salmon colored although white-nacred specimens occur. Pearly growths are not as common among the shells of this species as found in the region under consideration as among the same species from other places. A few individuals had blister and pin-head pearls. A specimen each of the type and the variety had a peculiar pearl formation on the pallial line at or near the posterior end of the shell. These are somewhat dome-shaped, about 5 mm. in diameter and 4 mm. in height and evidently were caused by an effort on the part of the mollusk to cover some irritating object, possibly a nematode worm (Figs. 31, 32). As both shells were without the animal (*pavonius* had been alive very recently) this point could not be determined. The *edentulus* was from the railroad bridge east of Sidney (No. Z11098) and the *pavonius* from below Homer Park dam (No. Z11144 A).



#### 14. *Anodonta grandis* Say. Floater.

The floater or paper-shell is more or less abundant in Salt Fork and other parts of the Big Vermilion drainage. In Spoon River it is common, living in the lower part of the stream. From this station to the station called bench mark 655, over five miles below, not a living *Anodonta* could be found, and the species does not become abundant until the cement bridge east of Sidney is reached, nine miles below Spoon River. This distribution is again indicative of the harmful influence of sewage on the bottom inhabiting animals. From the cement bridge to the Homer Park dam *grandis* is fairly common. It was very rare below the station at Homer Park, at which place it is common. The best habitat observed appears to be between the cement and railroad bridges east of Sidney, where the water is fairly deep in summer (three-four feet) and where there is a soft mud bottom and not much of a current in the stream. The species is typically a pond-inhabiting mussel. Gravid individuals were collected on September 13, 1918.

At Mahomet, on the Sangamon River, *grandis* is abundant and of large size, and occurs on a fine sand bottom. The Sangamon specimens are on the whole more cylindrical in form than those from the Big Vermilion and have a brown or brownish-green epidermis. The Big Vermilion specimens are mostly grass-green in color and are more elongate-ovate in form, the ventral margin being almost universally rounded while in the Sangamon shells this margin is nearly straight. The Sangamon River *grandis* are on the whole more solid than the same species from Salt Fork.

The nacre of the great majority of the Salt Fork specimens is bluish-white, while that of the Sangamon specimens is salmon-colored for the most part. A few individuals from both streams have salmon-colored patches and small pearl growths indicating that the animals had suffered from the attack of distomid worms, possibly the distomid of Osborn, which is known to infest this species in other places (Wilson and Clark, 1912). These shells, however, were rare and infection from this source seem uncommon among the *grandis* of these streams. No *Unionicola* (*Atax*) or other water-mites were observed in this species. These parasites are common in *grandis* inhabiting other streams (Wilson and Clark, 1912: 61-71).

An empty shell from the big bend in the Salt Fork showed evidences of distomid infection in the form of elongated blisters on the ventral margin of the valves, near the pallial line. In the right valve, near the anterior adductor muscle scar, there is a large blister, 8 by 12 mm. which evidently covered a distomid. The left valve of this specimen had suffered an injury when the animal was about two-thirds grown, which has caused a part of the antero-ventral margin to become folded inward, a part of the folded portion having the epidermis well preserved. The animal

continued its shell formation so perfectly that from the outside no evidence of an injury is visible. This shell indicates plainly a case of a hard struggle for existence against both mechanical injury and heavy parasitism. The interior of the shell is spotted with grayish patches and salmon-colored streaks (No. Z11029-A). (Figs. 22,23.)

#### 14a. *Anodonta grandis gigantea* Lea. Floater.

Specimens of an *Anodonta* from Crystal Lake, Urbana, are apparently referable to Lea's *gigantea*. Simpson (1914:420) diagnoses this variety as "Shell large, ovate or subrhomboid, a little higher in proportion to the length than the type; beaks full and high." The specimens from Crystal Lake agree with this diagnosis. The largest individual measures 152 mm. in length and 92 mm. in height. The umbonal region is more corpulent than in the *grandis* from the other parts of the Salt Fork. The color is brownish or greenish, the two colors frequently in alternating zones on the same specimen. Evidences of distomid infection are common in the form of salmon or pink discolorations and ridges. One individual has many long, thin, curved ridges on the interior of the shell, principally in the left valve. One of these ridges measures 93 mm. in length and 1.50 mm. in height (Fig. 24). Another individual has a round pearl attached to the posterior end of the shell, measuring 5 mm. in diameter. This variety has not been observed in any collections from the Big Vermilion or Sangamon rivers. Marsh has recorded *gigantea* from the Big Vermilion (Baker, 1906:73) but the exact location is not known, and must have been below the points examined by the writer.

#### 15. *Anodonta corpulenta* Cooper. Floater.

The large *Anodontas* from Crystal Lake are divisible into two groups; one is the variety of *grandis* described above; the other seems to be the *corpulenta* of Cooper, although the shells are smaller than examples of this species from other rivers. The shells referred to *corpulenta* are subrhomboid, somewhat elongated in a few of the individuals. The umbonal swelling is very pronounced, extending well downward on the shell. The anterior end is broadly rounded and the posterior end is distinctly plow-shaped and rather strongly biangulate. The epidermis is olive or brownish. The surface is very rough, the growth lines in some specimens being elevated into longitudinal ridges. As in *gigantea*, the inner surface is ridged and salmon-colored in many specimens due to the presence of distomid worms. No specimens of this species were seen which did not in some degree show evidences of the work of this parasite. Characteristic measurements of this shell are given below (Z11368):

Length, 127; height, 82; breadth, 53 mm.					
"	119	"	71	"	58 mm.
"	128	"	70	"	50 mm.
"	111	"	64	"	50 mm.

The large *Anodontas* in Crystal Lake are apparently not members of the original Salt Fork fauna. Neither *grandis gigantea* or *corpulenta* are found anywhere in the Big Vermilion drainage, at least above Middle Fork, 45 miles below Urbana. Since these shells were planted in the lake (see p. 27) they have evidently thrived and multiplied. *Anodonta grandis footiana* is parasitic in the glochidial stage on the Johnny Darters (*Boleosoma nigrum*, Hankinson, 1908:235) and as this fish also inhabits Crystal Lake it may have been the medium for the propagation of the alien fauna. That this fauna should have been so easily detected as alien is due to the method of examining a stream from its source to its mouth and the distinguishing of the foreign population is a striking recommendation of this mode of stream study.

**16. *Anodonta imbecillis* Say. Paper-Shell.**

This beautiful paper-shell occurs abundantly in but one place in the Salt Fork—near the cement bridge east of Sidney. Here it is of good size, grass-green in color, the rest periods showing as black longitudinal bands. The shell is easily known from all others in this State by the very flat umbonal region which is flush with the upper or dorsal margin of the shell. The largest specimen in the collection measures 75 mm. in length. *Imbecillis* was not collected or observed above the cement bridge, 19 miles downstream from Urbana. It was, also, not seen below the bed at Homer Park and it appears to inhabit only that portion of the stream between these points, a distance of about 8 miles. This mussel thrives best on a mud bottom in quiet water and it is not found, normally, on a sand or gravel bottom. It did not occur in our Sangamon River collections.

All of the individuals from Salt Fork bear evidences of distomid infection. In nearly all of the valves there are many small pearl-like blisters about the size of a pin head which are in all cases confined to the posterior two-thirds of the shell. None were noted near the anterior end.

The species is peculiar and almost unique among naiades in being hermaphroditic and in carrying the glochidia within the gills until they are ready for independent life, there being no parasitic stage encysted on fish as in the case of most Unionidae (Howard, 1914:353). It has an almost continuous breeding season, glochidia or embryos having been found in the gills during almost every month of the year. The Salt Fork specimens were gravid on August 26 and contained well formed glochidia. In this mode of reproduction *imbecillis* is paralleled by *Strophitus edentulus*, which also passes through its metamorphosis without parasitism.

**17. *Anodontoides ferussacianus* (Lea). Paper-Shell.**

This small naiad was found abundantly in but two places—the Middle Fork and Stony Creek near Muncie. It occurred infrequently at all other stations. In the upper Salt Fork, north of Urbana, it was common at one



time, near Lincoln Avenue, and in Crystal Lake. Two summers collecting failed to find it common at the present time at these places. Living specimens were not found in the Salt Fork between Spoon River and the big bend below the natural dam, a distance of over four miles, and it did not occur even infrequently above Homer Park dam, a distance of 17 miles.

All of the specimens collected are fresh, bright colored shells, greenish or olive with distinct grass-green rays. All but one specimen were normal in form and coloration. An individual from the cement bridge station was thicker than usual, had a short truncated posterior end and somewhat resembled small specimens of *Strophitus edentulus*. The beak sculpture was characteristic of *Anodontoides*. Pearly growths and abnormalities are rare in the shells collected. Gravid females were found September 26 and October 8. It seems to be rare in the Sangamon River, only a stray valve being found in this river near White Heath.

#### 17a. *Anodontoides ferussacianus buchaneensis* (Lea).

Specimens from the Salt Fork near Muncie and from the Big Vermilion are referable to this variety, long known under the name *subcylindracea* of Lea. The variety in the Big Vermilion drainage is more elongate, more cylindrical, and has a less height in comparison with the length than in the typical form. It is also decidedly biangulate behind, a characteristic lacking in the typical form. At the two localities it is associated with *ferussacianus*, but at Muncie it is the prevailing form.

#### 18. *Arcidens confragosus* (Say). Rock-Shell.

This species is a rare inhabitant of the Sangamon River and is not found in the Big Vermilion River. It was reported from the Sangamon River at White Heath and Monticello by Mr. James Zetek, about ten years ago. Professor Smith has not found it at Mahomet during many years of collecting. Recently (September 1920) a single specimen, dead, was picked up by the writer in the Sangamon River at a point about four miles above Mahomet, thus establishing its presence above White Heath. It probably lives sparingly in the river and may inhabit water too deep for examination. It has been reported from the Sangamon at Springfield (Baker, 1906:74).

#### 19. *Lasmigona (Platynaia) compressa* (Lea).

This characteristic species is rare in the Big Vermilion River. Several fine specimens were collected from the station three and a half miles above Homer Park in riffles on a sand-gravel bottom. One of these shells is pathologic, the umbones being almost in the center of the shell, the anterior end having a strong depression in front of the umbones. The posterior end is much shorter than usual and is rounded instead of broadly truncate. The interior shows distomid parasitism near the posterior end with a large elongated blister near the postero-ventral margin. The pseudocardinal in



the right valve is elongated and thinner than in normal individuals and the lateral teeth in both valves are scarcely visible. In the left valve there is an abnormally high, long and narrow tooth under the beak. There is a pronounced lunule in front of the umbones which is absent in typical *compressa*. This species occurs infrequently in mud at Homer Park. In the Middle Fork a single dead and broken shell was found. No representatives of this species were found in the Sangamon River.

**20. *Lasmigona (Lasmigona) costata* Rafinesque. Fluted Shell.**

This characteristic mussel is fairly common at most stations visited from bench mark 655 (fifteen miles below Urbana) down the stream to Middle Fork. It probably inhabits the lower Big Vermilion to the Wabash River. Living specimens, however, were not seen above the station four miles above Homer Park dam, nearly 23 miles from Urbana. From Homer Park down stream it is a common mussel. The individuals are for the most part fine, large, heavy shells with good clean lustre. The shells from Homer Park have an olive epidermis beautifully marked with green rays. The largest individual collected measured 145 mm. in length and was found at the station three and a half miles above Homer Park dam (Z11116A).

The majority of the specimens of this species are colored light salmon on the interior of the shell. Pathological individuals are rare in the collections. One specimen from Salt Fork near Middle Fork, found on a sand bottom, has a large pearl blister on the posterior margin. A shell from Homer Park, taken from a gravel bottom, has an injury in the form of a crack in the shell on the outside which had been repaired on the inside by the addition of pearly matter forming a long, raised blister, 45 mm. long and 2 to 5 mm. wide (Fig. 33). This nodulous blister reaches almost to the center of the shell (Z11192 A). Gravid individuals were collected on October 8 and 13, 1920.

The *costata* from the Sangamon River, where the species is common, are somewhat heavier than those from the Big Vermilion River. The shell is also less high in comparison with its length. Young individuals of this species from either river drainage are very rare, judging by our collections.

**21. *Lasmigona (Pterosygna) complanata* (Barnes). White Heel-Splitter.**

This large, roundish, flat mussel is the most abundant species in the Big Vermilion River, occurring commonly or abundantly in all parts of the stream, excepting a small stretch of about five miles near St. Joseph, from Spoon River to the neighborhood of Danville. It also probably occurs in equal abundance below Danville. The abundance of this species in Spoon River and below the station bench mark 655, with the break of five miles between the beds of living mussels, is strong evidence of the effect of sewage pollution. In this barren area only empty shells and odd valves could be

found after careful search; in one place, below the first bridge south of St. Joseph, dead, empty shells were abundant, but a careful search, conducted on two days, failed to discover a single living specimen. The largest and finest shells occur at Homer Park on a mud bottom in water from two to three feet deep. The largest shell from this station, a female, measured: length, 185; height, 130 mm. The species was observed to be gravid on the 6th of November, in 1918, and on October 8, in 1920.

The shells of *complanata* are very uniform in general shape, nacre, and condition. Pearly growths or pathological forms are rare. A few specimens contained small pin-head pearls and an occasional individual had suffered slight injury to the posterior part of the shell. The presence of many young and immature specimens indicates that the species is now breeding well and that the glochidia are finding suitable fish hosts. Young shells from the Sangamon River, where the species is abundant, are more of an olive color and not as green as those from the Salt Fork and other parts of the Big Vermilion River. Old shells from both drainages are dark brown or black.

## 22. *Alasmidonta* (*Pressodonta*) *calceola* (Lea).

This species has been recorded by Mr. Zetek from west of White Heath in the Sangamon River. No specimens were observed during the recent survey. As far as known it does not occur in the Big Vermilion River.

## 23. *Alasmidonta* (*Rugifera*) *marginata* Say. Elk-Toe.

In the big Vermilion River, this species is found, infrequently, at most stations from bench mark 655 as far down as the stream has been examined. It is not abundant anywhere and common at but three stations—below the dam at Homer Park, south of Muncie, and in the Big Vermilion. The first station where living specimens were found is four miles above the Homer Park dam. Individuals, both above and below the dam, are of good size and fine color, the characteristic green rays being very brilliant. Specimens from Middle Fork have many black spots on the shell. The largest specimen collected from the station two miles above the Homer dam, measured 80 mm. in length and 45 mm. in height; one from the Big Vermilion measured 96 mm. in length and 48 mm. in height.

*Marginata* exhibits little evidence of parasitism or abnormalities. One specimen collected from two miles above the Homer dam had several pearly growths and blisters indicating distomid infection. Gravid females were collected on October 8 and 13, 1920.

This species is rare in the Sangamon River, only one specimen being found at Mahomet during a days search. *Marginata* is a species more common in the upper waters of rivers and streams and is not, as a rule, found in any number in the larger rivers.

## 24. *Amygdaloniaias elegans* (Lea). Deer-Toe.

But one specimen of this peculiar species was found. This individual was collected by Professor Smith at the big bend below the natural dam. The specimen was an empty shell, iron stained outside and inside, and apparently had not been living for a considerable time. It is typical in form but not as large as individuals from the larger rivers. The measurements of this specimen are: length, 57; height, 47; width, 27 mm. That but one specimen of this species should have been collected in this river drainage seems quite surprising, indicating, probably, that the species has not been able to become established. It is not found in the Sangamon River as far as known.

## 25. *Obovaria circulus* (Lea).

This nearly circular mussel was collected at but five stations in the Big Vermilion River; Homer Park below the dam, near Muncie, Salt Fork near Middle Fork, in Middle Fork, and in the Big Vermilion below Middle Fork. It is infrequent at the first place and abundant only in Middle Fork, near its junction with Salt Fork, on a gravel and sand bottom, in fairly shallow water (September) and in the Big Vermilion (October). In the Big Vermilion this species is very uniform in shape and size, the ratios of height to length ranging between 70 and 90 per cent. The shells are usually nearly circular and have a distinct light yellowish-brown zone at the posterior margin. The nacre is pearly and there are no evidences of discoloration from injury or parasitism. It has not been found in the Sangamon River.

As in the case of so many of our mussels whose names have become familiar, this species may have to be changed to that of *subrotunda* Rafinesque (1820).

## 26. *Actinoniaias ligamentina* (Lamarck). Mucket.

This mussel was not found above the Homer Park dam. It occurred infrequently (almost rarely) below the dam on both a mud and a gravel bottom. In the Salt Fork near its junction with Middle Fork but one dead shell was found in half a days search for a distance of nearly a mile up stream. In Middle Fork, between the interurban bridge and the mouth of the stream, it was fairly common on a gravel and fine sand bottom in shallow water near riffles. In the Big Vermilion below Middle Fork it is the most abundant mussel, attaining a length of over 135 mm.

The individuals of this species are all normal specimens; the young and half-grown shells are greenish with many dark green rays of various width. Older shells are yellowish with few rays. In an old shell measuring 120 mm. in length and 75 mm. in height the rays showed but faintly (Z 11216). Evidences of distomid enfection were rare in this species in the Big Ver-



million specimens. A long narrow pearly blister on the posterior margin of one specimen might have been due to the presence of the marginal distomid described by Kelly. Clark and Wilson (1912:62) found this distomid common as cysts in *ligamentina* from the Maumee River. A specimen from the Big Vermilion had a large pearl-like blister at the lower edge of the posterior adductor muscle scar. (Z 11482 A). An abnormal shell without the animal, was found in Middle Fork. The posterior end is sharply truncated and bent inward in the right valve and bent outward in the left valve. The hinge teeth are much more elevated and heavier than in normal specimens. This abnormality was due to an injury received when the shell was about three years old. It must have lived upward of two years after receiving the injury, judging by the rest marks on the shell. This individual measures length, 84, height, 52 mm. (Z11216A).

The Middle Fork and Big Vermilion shells are thick and of good, clear, pearly-white lustre. The mucket is one of the most valuable shells for the cutting of button blanks and the Middle Fork and Big Vermilion specimens appear to be of excellent quality for this purpose. The species from this stream could be used for glochidial infection of fish. Gravid females were collected on September 26. *Ligamentina* was not found in the Sangamon River.

## 27. *Actinonaias ellipsiformis* (Conrad).

This small naiad occurs rarely at three places in the Big Vermilion River; below the dam at Homer Park, in the Salt Fork south of Muncie, and in the Big Vermilion below Middle Fork. Whether this rarity is due to a real scarcity of the mussel or to the inability of the collectors to find it, is not known. Diligent search was made in the various places visited, and the fact that but few specimens have been found by Professor Smith after years of constant collecting at Homer Park, leads to the conclusion that the species is rare in this stream.

*Ellipsiformis* is common in the Sangamon River at Mahomet where it occurs on a sand and gravel bottom, more commonly on riffles, where the current is rather swift. The shells from this station are not large (maximum size, length, 63, height, 31 mm.) but are very thick, with pearly-white nacre. The shape is normal, the posterior end being sharply pointed with a narrow truncation. The color is yellowish or greenish with many dark green rays, often wavy. Rest periods show as elevated longitudinal ridges, especially near the ventral margin of the shell. A half-grown specimen, length 38, height 23 mm., resembles in outline young shells of *Actinonaias ligamentina* and if found with that species would probably be so identified. *Ligamentina*, however, is not found at Mahomet, and this specimen is doubtless referable to *ellipsiformis*. Utterbach's reference of the species to the genus *Nephronaias* (= *Actinonaias*) is strengthened by the similarity of these shell characters, which this author has also noted (1916: 142).



In the largest specimen of this species, from the Sangamon River, the right valve has a large blister parallel with the postero-ventral border, measuring 17 by 7 mm., and anterior to this blister a group of twenty of more 'pin-head' pearls. There are several of these small pearls in the center of the valve. The left valve has a number of 'pin-head' pearls bordering the pallial line and one larger (1 mm.) black pearl in the center of the valve. (Z11230 A). These may have been caused by distomid parasites, although none were observed in the animals of this species. Only one shell in a dozen were thus affected.

## 28. *Carunculina parva* (Barnes).

This diminutive mussel is characteristic of the smaller tributaries of the Big Vermilion River. It occurs commonly in the ditch above Urbana and also in Spoon River. No living specimens were found between the Spoon River tributary and the station one mile above iron bridge north of Sidney, a distance of over six miles. From this station to the railroad bridge east of Sidney, a distance of three miles, this species was abundant or common. It is infrequent at Homer Park and was not found in the Salt Fork below Muncie or in Middle Fork. Its normal habitat in the Salt Fork is on a mud bottom in quiet water. At Homer Park, however, it occurs sparingly on a gravel bottom in very shallow water.

The species as found in Salt Fork is normal in form but not of large size, the largest specimen observed, from the railroad bridge east of Sidney, measuring 30 mm. in length and 18 mm. in height (Z11096). The surface in the Salt Fork specimens is rayless, the color being brown from the um-bones to the center of the valve, the balance of the shell being black. Specimens from Spoon River were smaller than those from farther down the stream.

*Parva* occurs infrequently in the Sangamon River at Mahomet on a mud or sand bottom.

## 29. *Carunculina glans* (Lea).

This small mussel, which is much higher in proportion to its length than *parva*, is very rare in Salt Fork, where it was found at but three stations, living individuals being collected only below the dam at Homer Park. Like *parva*, it is a species of the smaller tributaries and its normal habitat is on a mud bottom. It was not found in the Sangamon River at any station examined.

Frierson (1914: 7) has identified Lea's *glans* with the shell called *Unio* (*Toxolasma*) *lividus* of Rafinesque, changing the generic name, accordingly, to *Toxolasma* Rafinesque. In this he is followed by Ortmann (1918:572, 573). Should these names be plainly identifiable from the original descriptions, these small shells will bear the names *Toxolasma parvum* (Barnes) and *T. lividum* Rafinesque. The writer wonders whether

some of these Rafinesquean names have not been adopted too hastily and whether the fact of the identified specimens in the Poulson collection has not unduly influenced the references, which, without these identifications, are not as clear. The test must be, it would seem, a clear case of identification from the writings of Rafinesque alone.

### 30. *Eurynia (Micromya) lienosa* (Conrad).

The distribution of this small mussel seems to be coincident with that of *Lampsilis luteola* in the Big Vermilion and its tributaries. It occurred infrequently living in the Spoon River. It was not again collected in a living condition above the iron bridge north of Sidney, seven miles below Spoon River. At this place only one living specimen was found, and as far down as the cement bridge it is only infrequent. Between this point and the station three and a half miles above Homer Park dam no living specimens were found after diligent search in favorable habitats. It does not occur in any abundance above Homer Park dam; but below the dam the species is abundant and of large size. The largest specimens from Homer Park measure: length, 65; height, 31; breadth, 28 mm. (male); length, 55; height, 34; breadth, 25 mm. (female). In Salt Fork near its junction with Middle Fork it is abundant and in the Middle Fork it is common.

The species varies somewhat in coloration. From Homer Park upstream the color is black or dark brown with rarely faint indications of rays. Specimens from Middle Fork and Salt Fork near Middle Fork are more of a chestnut color, slightly reddish, often with quite distinct rays. By arranging the different lots by consecutive stations down the river it may be at once observed that there is a marked and striking increase in size, the increase being in some cases as much as 50 per cent between Spoon River and Homer Park. The Homer Park shells are on the average somewhat larger than those from farther down the stream and from Middle Fork.

The shells of many individuals of this species contain pearly growths in the form of blisters and 'pin-head' pearls. These occur near the margin of the valve, more frequently near the posterior end near the siphonal region. Gravid females were collected at Homer Park on July 30.

*Lienosa* was not collected from the Sangamon River and no records have been seen of its occurrence in that stream.

### 31. *Eurynia (Micromya) iris* (Lea).

A broken valve of this species was found in Middle Fork below the interurban bridge. The rays are distinct and the shell seems typical. It measures, length 37, height 21 mm. It appears to be a very rare shell in the parts of the Big Vermilion examined but may be more abundant

below the stations examined where the river is larger. *Iris* has not been recorded from the Sangamon River.

### 32. *Lampsilis luteola* (Lamarck). Fat Mucket.

The mussel known among fishermen as the fat mucket is common or abundant almost everywhere in the Big Vermilion and Sangamon rivers. It has been killed by the sewage of the Salt Fork from St. Joseph to bench mark 655, a distance of five miles down the stream, but the number of dead and empty shells found almost everywhere between these points indicates that at one time, not very remote, it was common continuously from Spoon River, where it now lives in some abundance, to the Wabash River. Below the dam at Homer Park it is very common and of large size, and this abundance continues down the stream and was also noted in the tributary Middle Fork. At Mahomet on the Sangamon River it is also abundant.

There is great variation both in form and coloration among the shells of this species in all of the habitats examined. The male shells are usually pointed at the posterior end and are elongated and somewhat compressed. From this form they vary by being quadrate in outline with a distinctly plow-shaped posterior end, corpulent and almost cylindrical, or flattened and oval, in this form greatly resembling *Actinonaias ligamentina*, from which they may be distinguished by the numerous double-looped ridges on the umbones. The female shells do not differ so greatly in shape, the post-basal swelling for the accommodation of the enlarged branchial marsupium giving more uniformity to the shell, the variation being principally in the width of the shell, which in old specimens is very pronounced. Male shells greatly predominate in the collections. In color there is every gradation between a bright yellow shell with distinct, narrow dark green rays, to a shell that is dark yellowish or brownish without rays or with the rays only faintly developed. A few specimens are dark brown or even pinkish with narrow, greenish rays. Young shells are very brightly rayed, the rays being dark grass-green on a light yellowish background, forming a beautiful surface ornamentation. The rays on the adult shells may be narrow or broad, or the broad rays may be made up of many fine rays, which may also be a trifle wavy. The nacre in all specimens examined from the two rivers here considered is pearly white, unmarked by color of any kind. The largest specimens seen occur at Homer Park; measurements of these are given below:

Length, 110;	height, 59;	breadth, 35 mm.	Male
" 116	" 68	" 40 mm.	Male
" 116	" 69	" 46 mm.	Female
" 100	" 65	" 48 mm.	Female

Pearly growths were observed in many of the specimens collected. Occasionally a few pin-head pearls occur in a valve but the greatest number



of abnormalities consist of cyst-like pearly growths near the posterior end, in or near the adductor muscle and pallial line. These may occur in one or both valves. Occasionally the anterior adductor scar is almost wholly changed in character by these abnormal growths. In several shells the space between the pallial line and the margin of the valve is stained purple or brown, accompanied by few or many blisters of various sized. The posterior end of the shell may also be affected so that it ceases to grow, forming a blunt posterior end marked by blisters and discolorations. Whether this condition is due to distomid infection as mentioned by Wilson and Clark (1912:63) as occurring in *Actinonaias ligamentina* from the Maumee River is not known definitely, but the inference is strong that it is. It is noteworthy that the largest number of individuals affected by parasitism or other injurious agencies occurred in the upper part of the Salt Fork above Homer Park dam. Specimens collected from stations below the dam, including Middle Fork, were as a whole remarkably free from pearly growths or discolorations. Occasional individuals from Mahomet, on the Sangamon River, have round, pin-head pearls in the shell. Though no distomids were observed in the animals of *luteola* it is quite probable that these pearls and blisters, which were observed for the most part in empty shells, were caused by distomid larvae, possibly the marginal cyst described by Wilson and Clark (1912:62). Many young shells of *luteola* were collected and many more observed, indicating that the species is breeding freely from the Homer Park section of the stream downward. No young shells were seen above the Homer Park dam. Gravid females were observed at several places in September and October.

A specimen collected at Mahomet (Z11223 A) somewhat resembles *Actinonaias ligamentina* in the form of the shell, absence of strong umbonal markings and heavy hinge teeth; it seems to be one of those individuals which has led many students to say that "*ligamentina* runs into *luteola*." The shell is free of all abnormalities and has a clear pearly-white nacre. It measures, length 87, height 54, breadth 30 mm.

### 33. *Lampsilis ventricosa* (Barnes). Pocket-Book.

This large fine species was not collected in Salt Fork above the station about two miles north of Sidney, 16 miles below Urbana. As it does not occur in Spoon River (as far as known from our collections) it is probably a species that does not inhabit the smaller tributary streams. From the station mentioned as far down stream as the river has been examined, including Middle Fork, *ventricosa* is common or abundant in most places. Below Homer Park dam it is abundant and of large size, and more or less ponderous. The largest female shell was found at Homer Park and the largest male shell in Salt Fork near Middle Fork. These shells measure as follows:

Length, 138;	height, 60;	breadth. 56 mm.	Male
" 117	" 60	" 60 mm.	Female



Shells from the Sangamon River are equally large.

The shape of the shell is fairly constant and there is little variation except in the females, which are rounder posteriorly and have a large post-basal swelling for the enlarged marsupia. In color the Big Vermilion shells are all yellowish with dark green rays on the posterior slope. No specimen was seen in this river that was rayed all over. Very old specimens are entirely rayless. At Mahomet, on the Sangamon River, the yellow shell occurs and also another form in which the shell is yellowish-green with bright, grass-green rays, often of considerable width. One specimen is in outline like *Actinonaias ligamentina* and the surface is densely covered with dark green rays. Two other specimens have green rays on a pink background, have pink hinge teeth, and the whole interior of the shell is pinkish. These bright colored shells are the form called *occidens* by Lea.

These pink shells and the specimens with the numerous green rays are so strikingly different from the *ventricosa* as found in the Big Vermilion and also from the other shells found in the Sangamon, that the name *occidens* might be retained for these shells for ecological purposes. The color is not an age stage, for young yellow *ventricosa* were found associated with these distinctly rayed forms, and the rayed forms were collected at Mahomet and were not found at White Heath in the Sangamon. The river below Mahomet has not been carefully searched, however, and the *occidens* form may occur in some of this unexplored territory. It is also to be noted that, as far as the material from these two rivers is concerned, the beak sculpture of the *occidens* type of shell is very much larger and coarser than in the *ventricosa* type (Z11222). This form falls under the group of individuals called mutations by DeVries and others.

Ortmann (1918:583) makes *ventricosa* a variety or race of *ovata* (Say). As far as the authors' experience goes, this seems unwarranted, the two species being as easily separable as many other closely allied species. Individual specimens from Illinois localities approach *ovata* in that the posterior ridge is somewhat accentuated, but no specimens have been seen that could not be placed readily in one species or the other. *Ovata* is reported from the Ohio River in Illinois by Marsh but this species is more southern in its distribution, reaching its maximum development in Alabama and Tennessee. *Ventricosa* is a more northern species attaining its maximum development in the rivers of Illinois and Indiana.

*Ventricosa* is subject to the attack of distomid worms as well as to parasitism by mites (*Unionicola*) and the material of this species from the Big Vermilion have suffered more or less from this cause. Blisters, pin-head pearls and various abnormalities occur in many individuals. Among the shells collected at the station one mile above iron bridge north of Sidney there are several individuals of this sort. One has a large blister extending nearly the whole length of the ventral margin and covering the

space between the margin and the pallial line. This was evidently formed by distomid parasites (Z11058 A). Another specimen from the same lot (Z11058 B) has a large group of pearls (over 100) filling the space between the ventral margin and the pallial line over an area of about two inches. Other specimens have an abnormally thickened ventral margin in addition to blisters, indicating the presence of some irritating material between the shell and the mantle lobes, probably mud or sand (Z11149 A). A specimen from Mahomet had suffered a curious injury which had caused a large blister extending from the upper third of the posterior end to the center of the ventral margin, a distance of about three inches. This was plainly due to the presence of a quantity of mud getting in between the shell and the mantle, a small amount of this material being retained under the cylindrical blister on the ventral margin. The outside of the shell was so perfectly repaired that there was no evidence of the pathological condition within the shell (Z11202 A). Fig. 35. This injury was only in the left valve, the right valve being normal.

Nearly all of these pearly growths, blisters, and abnormalities have been noted to occur almost universally without the pallial line, between this muscle attachment and the ventral, anterior, and posterior margins of the shell. This limited area is easily understood when it is remembered that the adductor muscles and the pallial line form a barrier to the entrance of foreign material because the muscles at these points are firmly attached to the shell and parasites or foreign material cannot readily gain entrance to the interior of the animal between the mantle and the shell. This is true of all the shells of other species examined from these two river systems. It was noted that pearly growths and abnormalities were rarer in the shells from the Middle Fork and from Salt Fork near the Middle Fork than from Homer Park and up the stream from this habitat. The shells from the Sangamon River at Mahomet were much less subject to parasitism or abnormalities than those from the Big Vermilion River.

Young shells of *ventricosa* were common only in Middle Fork, in Salt Fork near Middle Fork, and in the Sangamon River at Mahomet. No young shells were collected from the stream above the dam at Homer Park.

Gravid females were observed on September 26 in the Salt Fork near Middle Fork in the act of spawning. The shells were buried in the sand, only the tips of the siphons showing above the general level of the bottom of the stream. The bright yellow siphon fringes, which are enlarged during the spawning period, were observed to wave about with graceful undulatory motion. The movements were more or less intermittent, a waving period being followed by a resting stage. These mussels had well formed glochidia and were evidently discharging the embryos from the marsupia. These glochidia are of the hookless type and develop in the mouth of fish and the undulatory motions possibly attract these fish which may be thus

more easily infected with the glochidia, as suggested by Wilson and Clark (1912:13, 14). This undulatory motion of the siphon fringes is so striking that it at once attracts the attention of an observer, even if this person is not interested in the study of these creatures. Its habit of burying itself so deeply in the mud or sand of the bottom (four to seven inches) renders this species difficult to collect, especially if the sand be packed rather hard and the water is eighteen or more inches in depth, as frequently occurs. This condition was found in several of the Salt Fork habitats. Gravid females were also collected from other localities in October.

### 34. *Lampsilis multiradiata* (Lea).

This handsome mussel occurs rarely at but three stations, Homer Park, near Muncie, and in Middle Fork. It is common in the Big Vermilion below Middle Fork. The specimens from the Salt Fork Stations are all small for the species, being not over half the size of individuals from White River, near Muncie, Indiana, and the hinge teeth are much weaker than those from Indiana streams. This is especially true of the pseudo-cardinal teeth which are narrower and more elongated than the specimens examined from other streams. Individuals from Homer Park are brilliantly rayed, grass green on a yellowish ground. Middle Fork specimens are not as brilliantly rayed, the general color being yellowish with scanty rays. The largest specimens collected measure as follows, a specimen from Muncie, Indiana also being included for comparison:

Length, 34;	height, 22 mm.	Homer Park.
" 43	" 31 mm.	Middle Fork. Male
" 69	" 55 mm.	Big Vermilion. Female
" 85	" 64 mm.	Muncie, Ind. Female

This species is rare in Illinois waters, judging by the few records available. These indicate, however, a wide range over the State, from Cook County to southern Illinois (Baker, 1906:64). Ortmann (1918:584, 1920:309) adopts the name *fasciola* of Rafinesque (1820) for this species, stating that the original description of Rafinesque is definite enough to indicate without much question a shell of the *multiradiata* type. If this be so, then Lea's very appropriate name must give place to the one used at an earlier date by Rafinesque. The species has not been recorded from the Sangamon River.

### 35. *Lampsilis anodontoides* (Lea). Yellow Sand Shell.

This fine shell, which is usually abundant throughout Illinois waters, was collected at only three stations in the Big Vermilion River, all of which were below the dam at Homer Park. The largest and finest individuals occur at Homer Park and the smallest were collected in Middle Fork. Specimens from the first named station have a yel-



lowish shell with little or no indication of rays. Middle Fork specimens include yellowish shells without rays, as well as, more rarely, individuals with rather bright, wide rays, approaching in this respect the related species *fallaciosa* of Simpson. The largest specimens from the two localities measure as follows:

Length, 124;	height 57;	breadth 47 mm.	Male, Homer Park.
" 90	" 41	" 33 mm.	Female, Middle Fork.

The nacre is tinted with pinkish or salmon color. Pearly growths are not uncommon in specimens from the Big Vermilion. These are in the form of blisters and pin-head pearls, which are usually confined to the margin of the shell between the pallial line and the external margin of the valve. One individual from Homer Park had the entire area between the pallial line and the ventral margin of the shell abnormally enlarged and thickened, due possibly to the presence of distomid larvae and to some extent to the intrusion of small amounts of soil between the mantle and the animal (Z11147A). Specimens from Middle Fork are, as a rule, free from pearls and abnormal growths. Gravid females were found on September 26 in Middle Fork, and on July 30 in Salt Fork at Homer Park. *Anodontoides* has not been recorded from the Sangamon River at Mahomet or in the other places examined.

The early writers, Say, Conrad, and others, have identified this species with the *Elliptio teres* of Rafinesque (1820) and if the shell is clearly identifiable from the description of Rafinesque the familiar name of *Lea* must become a synonym.

### 36. *Truncilla* (*Pilea*) *perplexa rangiana* (Lea).

Four specimens of this race of *perplexa* are in the naiad collection of the Museum of Natural History, University of Illinois, collected by Mr. A. A. Hinkley, in the Big Vermilion River at Danville. Three are females and one is a male. They are much smaller than specimens from Florence, Alabama, where the species attains its greatest development. The male and largest female shell measure as follows, corresponding measurements being also given for the Alabama shells.

Length, 41;	height, 29;	breadth, 22 mm.	Danville, male, Z3770.
" 44	" 34	" 20 mm.	Danville, female, Z3770.
" 55	" 43	" 32 mm.	Alabama male, Z3947.
" 73	" 53	" 35 mm.	Alabama female, Z3947.

As no specimens of *Truncilla* were found in the Big Vermilion or its tributaries as far down as Middle Fork, which is but a few miles west of Danville, this species evidently does not inhabit the stream above the locality from which Hinkley collected his shells. *Truncilla perplexa* as well as its variety *rangiana* is known in Illinois only from the Ohio



and Wabash rivers. The small size of the Danville specimens may be due to the fact of their inhabiting the upper part of their distributional range, in a rather small river. Rafinesque's name *torulosa* has been used by Conrad, Agassiz, Reeve, and Ortmann for *Truncilla perplexa* and if the original description is clear enough to reasonably fix the shell as Lea's *perplexa* this form will stand as *Truncilla torulosa rangiana* (Lea). Neither *perplexa* or *rangiana* are known from the Sangamon River.

FAMILY SPHAERIIDAE

**37. *Sphaerium striatinum* (Lamarck). Variety.**

This finger-nail clam occurs abundantly only in the ditch north of Urbana. It also occurred infrequently in Spoon River, and near the iron bridge in Salt Fork north of Sidney. Dead specimens were found at bench mark 655 and below the Homer Park dam.

Sterki remarks of this form "possibly a form of *striatinum* Lam; apparently the same as a *Sphaerium* from Iowa and other places which for many years has been left unnamed, except in manuscript. It still seems impossible to say where the limits of *striatinum* are." The writer fully agrees with Dr. Sterki regarding the variation in this common species. This variety appears quite distinct from the ordinary specimens of the species and it is to be hoped that Dr. Sterki will give it a name. It is noteworthy that the form occurs commonly only in the drainage ditch above Urbana and was not found in any numbers below this place. A *Sphaerium* identified as *striatinum* by Zetek some years ago, occurring in Crystal Lake, was doubtless this form.

**38. *Sphaerium stamineum* (Conrad).**

This small mussel is abundant at several places in Salt Fork above Sidney. It occurs only infrequently at two other places. Reported by Zetek from Crystal Lake. Some of the shells are typical but others are similar to *striatinum* and it is difficult to separate some specimens from that species. At the station called bench mark 655 a form of this species occurs that is somewhat like the variety *forbesi* Baker, described from Mason County, Illinois.

**39. *Sphaerium solidulum* (Prime).**

An abundant species in the Spoon River and in the Salt Fork above Sidney. Occurs rarely at other places. Reported by Zetek from Crystal Lake. On the whole this species is quite uniform in characters.

**40. *Sphaerium* species.**

A *Sphaerium* occurs abundantly in Salt Fork below the Homer Park dam which is thought by Sterki to be possibly a new species. It is related to *solidulum* but is larger and more robust (mus. no. Z11383). It lives in

shallow water on a more or less rocky bottom a short distance below the dam.

**41. *Musculium transversum* (Say).**

This fragile finger-nail clam is apparently rare in Salt Fork and its tributaries, occurring only in Salt Fork near Sidney. It has been reported from Crystal Lake by Zetek. The specimens are typical.

**42. *Musculium truncatum* Linsley.**

This very small clam was found only in the old river bed near the cemetery north of Urbana. Here it is common and typical.

**43. *Musculium partumeium* (Say).**

Reported by Zetek from Crystal Lake. It has not been found recently.

**44. *Pisidium compressum* Prime.**

This small clam occurs in abundance only at the iron bridge north of Sidney. A few specimens were found below the natural dam in Salt Fork. The individuals are quite typical.

**45. *Pisidium kirklandi* Sterki.**

A single specimen of this species was found at the iron bridge north of Sidney. It is apparently very rare.

**46. *Pisidium splendidulum* Sterki.**

A few specimens of this tiny species were found in the Salt Fork near Muncie. The individuals are young and not quite typical.

The distribution of the Sphaeriidae in Salt Fork is interesting and significant in connection with the sewage pollution of the stream. It will be noted that no Sphaeriidae were found in the Salt Fork between the Urbana ditch and the station called natural dam, 14 miles below Urbana. These mussels are characteristic mud dwellers and their absence from the intervening territory in the stream is striking evidence of the unfavorable conditions on the bottom. They were not found in abundance above bench mark 655. It will also be noted that Sphaerium appears, living, before Pisidium and is also found in abundance higher up the stream. This may mean that Sphaerium is better able to withstand these adverse conditions than Pisidium, which is more of a mud dweller. Pisidium is much less common everywhere in the stream and but one species occurs abundantly at one place (Table IV).

FAMILY PLEUROCERIDAE

**47. *Pleurocera elevatum* (Say).**

This long-spined snail is rare or wanting in most parts of the Big Vermilion River. Two white, weathered specimens of this species were found below the natural dam in Salt Fork. They may have been washed

from a post-glacial fossil deposit. None were found either alive or dead in any other part of the Big Vermilion examined, excepting the two specimens mentioned above.

In the Sangamon River, at Mahomet, *elevatum* is very abundant on a sandy bottom in water a foot in depth (low water period). The specimens are large (maximum length 35 mm.) and vary in color from light yellowish to black or dark chestnut with a light zone below the suture. The characteristic peripheral keel is developed on the majority of specimens and ascends the spire just above the suture. In a few individuals this keel is absent and the body whorl is rounded. Many intermediate forms occur connecting these rounded shells with the more distinctly keeled forms. Usually there are from one to six spiral ridges on the base of the shell extending longitudinally parallel with the peripheral keel. The strongly carinate whorls of the young shell are six in number and these lose their sharpness more or less abruptly on the seventh whorl. No individuals were seen in which the protoconch or nucleus of the first whorl was preserved. Young and half-grown specimens have two brown bands on the spire whorls and four bands on the body whorl and base of the shell. This species also occurs in the Sangamon at White Heath, and it has been found in several Pleistocene deposits near Mahomet, the white shells of the fossils being washed out of the bank by periods of high water.

#### 48. *Goniobasis livescens* Menke.

This river snail occurred in but four places in Salt Fork. It was infrequent at bench mark 655 and abundant just below the dam at Homer Park and near Muncie. It is abundant in the big Vermilion below Middle Fork. It has been identified by local naturalists as *Goniobasis pulchella* Anthony and has been reported as this species by other students as from the Big Vermilion River (Baker, 1906:98). Specimens were sent to Mr. Calvin Goodrich, who is making a study of this family, and were identified as *livescens*. I quite agree with Mr. Goodrich that they are *livescens* rather than *pulchella*. Young and immature specimens are banded like *Goniobasis depygis* Say.

*Goniobasis semicarinata* Say is reported from the Big Vermilion River by Marsh (Baker, 1906:98) but no specimens have been seen from this stream. The species may live in the river below Danville or the citation may be based on long-spined *livescens*.

#### FAMILY AMNICOLIDAE

#### 49. *Pomatiopsis lapidaria* (Say).

This tiny snail is abundant in small, cold streams flowing into the Sangamon River. At one locality, about three-fourths of a mile below Mahomet, it was extremely abundant in a small brook about two feet



wide and not exceeding six inches in depth. The bottom was of mud and fine sand. The largest specimen measures 7 mm. in length. This species was not collected from streams flowing into the Big Vermilion River.

**50. *Amnicola limosa* (Say).**

This common *Amnicola* occurred at three stations, only two of these yielding living specimens. At the station above the iron bridge north of Sidney, the shells were secured by sweeping the vegetation bordering the shore with the Walker dredge. The *limosa* from the Salt Fork are rather corpulent but are not as globular as the variety known as *porata* (Say). It is noteworthy that this species (and in fact the genus) should be found only in a stretch of the stream three miles in length, from 16 to 19 miles below Urbana. None were seen below the dam. Individuals were rare and difficult to find. Near the cement bridge east of Sidney, dead shells occurred among water plants (*Nymphaea advena*) but no living specimens could be found. *Limosa* was not collected at the stations in the Sangamon River.

**51. *Amnicola* (*Cincinnati*) *cincinnatiensis* (Anthony).**

This *Amnicola* occurred rarely, but living, at but two stations in the Salt Fork, 16 and 17 miles below Urbana. The largest and only adult individual collected measures 6 mm. in length. Several half-grown shells were found. About two years ago Mr. James Zetek found *cincinnatiensis* near St. Joseph. A careful search of this region, both in the Salt Fork and in the small streams flowing into Salt Fork, failed to produce a single specimen of this species. During the intervening ten years the species appears to have died out, either from the effect of sewage pollution or from some other unknown cause.

FAMILY VIVIPARIDAE

**52. *Campeloma rufum* (Haldeman).**

The *Campelomas* of the Big Vermilion all appear to be referable to Haldeman's *rufum*. The shell is more or less pinkish, especially on the spire. One specimen from the iron bridge north of Sidney resembles Haldeman's figure 1 on plate 3 of the Monograph, which is the type of *rufum*. Specimens from Homer Park, below the dam, are strongly suggestive of *integrum* (Say), many of the individual shells being like Binney's figure 96 which represents Say's *integrum*. With these are short-spined shells recalling the *obesum* of Lewis as figured by Binney (figure 95). These are not quite like the figures of Lewis (1875, pl. 23, figs. 4-5) which are rather broader. Variation in *rufum* seems to parallel that of *integrum* in the length of the spire. Typical *integrum* has a white aperture and a bright green shell devoid of the peculiar pink tint of *rufum*.



The *rufum* from Homer Park have the spire whorls more or less gibbous, strongly shouldered, the first three whorls seeming to be telescoped into the later whorls. In this respect they resemble *integrum obesum* as suggested above. Measurements of a few of the Homer Park specimens are given below (Z11168):

Length, 37; breadth, 24; aperture length, 21; breadth, 14 mm.							
"	33	"	22	"	"	19	" 13 mm.
"	30	"	21	"	"	18	" 12 mm.

To this and other lots of *Campelomae* from the Big Vermilion River the statement of Lewis may be well applied: "These and many other forms in my collection, all part of a series, go far to show that it is unsafe to attempt to decide the limits of species from a few individuals" (1875:337).

The distribution of this species in Salt Fork is interesting and suggestive. Living specimens, small and few in number, were found over two miles upstream in Spoon River. Dead, mostly old and bleached shells, were collected at nearly all stations in the Salt Fork, but living shells of *rufum* were not seen above the station two miles north of Sidney. Here only one living specimen could be found. A mile farther down the stream another living specimen was collected. The presence of so many dead shells with so few living individuals above the Homer Park dam indicates clearly an unfavorable environment. There are many normal and favorable habitats for this mollusk in this stretch of nearly twenty miles in Salt Fork and the unfavorable agencies must be wholly those contributed by Man—the disposal of sewage and other wastes by means of this stream. Below Homer Park dam the species is abundant and as fine as can be found anywhere. *Rufum* is rare on a sand and gravel bottom and abundant on a mud bottom.

The *Campelomae* from the Sangamon River at Mahomet are also referable to *rufum*. The spire is longer and the shell narrower, however, than in the Salt Fork specimens, and there is no tendency to vary toward the *obesum* form of shell. The interior of the aperture is slightly pinkish. One specimen from Mahomet has a very heavy shell recalling the *subsolidum* of Anthony, a common species in most parts of Illinois but absent from either of the rivers under consideration. Reversed individuals are rare, only one specimen being found in the Sangamon River, a mile below Mahomet. This is a young individual.

The air-breathing snails, belonging to the genera *Physa*, *Ferrissia*, *Planorbis*, and *Galba*, are better able to withstand the ill effects of sewage and other stream pollution than are their relatives, the snails and clams that take their oxygen directly from the water (dissolved oxygen). They were therefore found in Salt Fork in places where the water breathers were entirely wanting, as at St. Joseph and the first stations below. It has

been observed in other places, notably in the Genesee River, at Rochester, N. Y., where sewage pollution was at one time very severe, that these pulmonate water snails were the last to succumb to the toxic influences of pollution and they have been known to live in water that was filled with putrescent matter and also in water strongly impregnated with arsenic. When these snails begin to disappear, conditions must indeed be deplorable.

#### FAMILY ANCYLIDAE

##### 53. *Ferrissia rivularis* (Say). River Limpet.

The tiny limpet-like shell known as *Ancylus* (*Ferrissia*) *rivularis* was very abundant in parts of Salt Fork, its usual habitat being the inside of empty valves of the naiades. The individuals are large (6.4 mm. in length) and fine and apparently normal in form. This species was found alive at St. Joseph where pollutional conditions are bad, and was also abundant at the stations lower down the stream where living mussels or pectinibranchiate snails were very rare or absent. Ancyli were not observed in Spoon River, in Middle Fork, or below the dam at Homer Park. Found by Mr. Zetek in the Sangamon River at White Heath.

##### 54. *Ferrissia tardus* Say. River Limpet.

This *Ancylus* is in the author's collection from White Heath and Monticello, Sangamon River, and from the Salt Fork near Urbana, collected by Mr. Zetek and identified by Dr. Bryant Walker. No *tardus* were collected during the present survey.

##### 55. *Gundlachia meekiana* Stimpson.

Specimens of this characteristic mollusk are in the author's collection from Crystal Lake, Urbana, collected by Mr. Zetek in August 1904, and identified by Dr. Walker. None were seen during the present survey.

In the catalogue of the Mollusca of Illinois (Baker, 1906: 101, 102) *Ancylus* (*Ferrissia*) *shimekii* Pilsbry is recorded from Salt Fork, Urbana, and *Ancylus* (*Laevapex*) *kirklandi* Walker from Crystal Lake, Urbana. These species were contained in the collection of the State Laboratory of Natural History. A recent examination of the material upon which these records are based indicates that there has been an error in the habitat given. None are from the Salt Fork or Crystal Lake. *Ancylus kirklandi*, identified by Walker, is in the laboratory collection from Havana, Illinois River (Nos. 13792, 13811, 24123) and Elizabethtown, Illinois (No. 24527). *Ancylus shimekii* (No. 24541) is in a bottle with *Ancylus rivularis*, both identified by Walker. The bottle is without locality and no record was found in the laboratory catalogs of the specimens bearing this number. It is evident, therefore, that these species of *Ancylus* must be eliminated from the list of the fauna of Salt Fork.

## FAMILY PHYSIDAE

**56. *Physa gyrina* Say. Tadpole Snail.**

This snail is usually abundant wherever found. In the old cut-offs of the Salt Fork above Urbana, as well as in the ditch north of Urbana, it is abundant and quite typical with long, slender shell and spire, the immature individuals with a short, dome-shaped spire. Below St. Joseph, where it occurs sparingly, the shell is broader and even in adult specimens the spire is more or less dome-shaped. *Gyrina* is more common above than below the dam at Homer Park. The species is more characteristic of slow-moving, pond-like bodies of water than of larger streams. It occurs also in Stony Creek near Muncie, in a small pond near Middle Fork, and in the Big Vermilion below Middle Fork.

**57. *Physa crandalli* Baker.**

Specimens of a *Physa* with a shouldered whorls, a wide body whorl, the shell thick and heavy for the genus are referred to *crandalli*. This mollusk is abundant in the drainage ditch above Urbana associated with *gyrina*. None were found in the cut offs of the old stream and the species probably does not inhabit the pond-like habitats in which *gyrina* is usually found, preferring running water. The specimens referred to *sayii* Tappan, from Urbana (Baker, 1906:99) are also this species. It is noteworthy that living specimens of this species were collected at St. Joseph where polluted conditions are bad. None were found below the iron bridge one mile north of Sidney, or in any part of the Salt Fork below this point. Characteristic specimens were collected in the Big Vermilion below Middle Fork, on a stony bottom in riffles.

## FAMILY PLANORBIDAE

**58. *Planorbis* (*Helisoma*) *trivolvis* Say. Wheel Snail.**

This species of wheel snail is apparently not common in Salt Fork, only scattering specimens being found along the stream. It occurred more abundantly in a small stream, dry in summer, which runs through low, swampy ground on the east bank of Salt Fork south of the interurban bridge at St. Joseph. Living *trivolvis* were not found in the stream above the first bridge below St. Joseph, twelve miles below Urbana. Even this air-breathing snail seems to be unable to live in any abundance in the polluted water of South Fork.

**59. *Planorbis* (*Helisoma*) *pseudotrivolvis* Baker.**

This recently described wheel snail (Baker, 1920:123) occurs abundantly in the old stream bed (cut-offs) of the Salt Fork near the Woodlawn cemetery, Urbana, and it is here the predominating species of the genus, true *trivolvis* being rare. The differences between this species and *trivolvis*



have been clearly pointed out in the paper referred to above. Two specimens, one living, referable to this species were found in Salt Fork about two miles below St. Joseph, associated with typical *trivolvus*.

**60. *Planorbis (Helisoma) antrosus* Conrad.**

A single, small, bleached shell of this species was found near the cement bridge northeast of Sidney. It may have been washed from a Pleistocene fossil deposit near by. None were collected living.

**61. *Planorbis (Gyraulua) parvus* Say.**

This small species was found in limited number associated with *Planorbis trivolvus* and *Galba parva* in the low ground subject to spring overflow south of the interurban bridge at St. Joseph. It was typical in form as compared with authentic specimens collected near Philadelphia by Dr. H. A. Pilsbry. None were found in Salt Fork or in the Sangamon River.

FAMILY LYMNAEIDAE

**62. *Galba parva* (Lea).**

This tiny pond snail was found at but one place in the Salt Fork. A dead shell was obtained at the iron bridge, a mile north of Sidney. In the low ground south of the interurban bridge at St. Joseph before referred to, *parva* occurs abundantly in the bed of a small stream which has water in it only in spring and early summer. On the Sangamon River, this species was noted in abundance on wet mud flats bordering the margin of the stream. This locality was about three-fourths of a mile below Mahomet. The polluted water at St. Joseph appears to have little effect on this species or the other pulmoniferous mollusks associated with it. It is probable that at the times of high water so much oxygen is mixed with the upper layer which overflows these low places that the ill effect of sewage pollution, from decomposition of organic matter, is so reduced in quantity and quality as to be little noticed by these air-breathers.

**63. *Galba humilis modicella* (Say).**

This is usually a very common species where it occurs at all. It is rare, however, in the Big Vermilion, scattered specimens, mostly dead shells, being found at four stations. It was collected living in the drainage ditch above Urbana, in Crystal Lake (Zetek), and a large typical individual was found alive on the mud bordering the stream a short distance below the mouth of Spoon River in Salt Fork west of St. Joseph. The species occurs sparingly in the Sangamon River associated with *Galba parva* at the locality mentioned under that species. In a small pond in the gravel pit north of the interurban tracks west of the Middle Fork, *modicella* occurs living among cat-tails (*Typha*) associated with *Physa gyrina*.



**64. *Galba obrussa* (Say).**

*Obrussa* occurs in Stony Creek near Muncie, collected by Mr. John R. Malloch, May 29, 1919. The specimens are typical though small.

**65. *Galba caperata* (Say).**

This species occurs abundantly in swampy woodlands bordering the Salt Fork about three miles north of Urbana, the ground in dry weather being almost paved with the dead shells of this snail. Some of the snails escape the dry period by crawling into cracks and holes and there hibernating. This species has not been found in or near Salt Fork or the other tributaries of the Big Vermilion River. Because of its preference for small, summer-dry ponds and pools this *Galba* will not be found, probably, in any part of the streams herein considered.

## POLLUTION OF SALT FORK BY SEWAGE AND MANUFACTURING WASTES

### GENERAL NATURE OF STREAM POLLUTION

Stream pollution may be broadly divided into two main divisions: contamination by organic sewage from cities and towns and by chemical wastes from factories and mines. Both are inimical to life but the latter is especially fatal to animal life, causing wide stretches of otherwise fertile streams to become veritable deserts. Organic sewage, in a crude or highly concentrated form, is also very injurious, effectually eliminating most forms of life from the polluted body of water.

The importance and seriousness of the problem of stream pollution in its effect on the life of the rivers and streams into which the contaminating material is discharged has not until very recently been given the attention the subject demands. The diminishing fish supply, and in many places the very objectionable physical character of the polluted waters, have caused the authorities of several states to pass laws governing the discharge of these wastes into streams and the establishment of penalties for disregarding these laws. New York and Massachusetts have led in the framing of these laws and other states are following the good example set by these two older commonwealths, where the conditions seem to have reached a maximum of harmfulness (see Ward, 1918, 1919).

During recent years stream pollution has enormously increased and the problems arising from this condition have been investigated by many biologists and sanitary engineers. The former have studied the problem from the viewpoint of its effect on the useful animal life, especially fishes and river mussels, and this phase probably bears as close a relation to human welfare as any other. Of course, from the standpoint of health, the pollution problem is of paramount importance because of its bearing on such diseases as typhoid fever which may be caused by a polluted water supply.

Perhaps the worst effect of chemical pollution is to be found in the streams of western Pennsylvania, where water heavily loaded with oil or acid water from coal mines is permitted to flow into the rivers and streams of this part of the state. Studies by Ortmann (1909) show that whole stretches of the Allegheny, Ohio, and Monongahela rivers have been made into deserts, as far as the animal life is concerned, by the large amount of poisonous substances discharged into these streams by the mines, oil indus-

tries, and chemical and other factories that border these rivers. In the Susquehanna River the same condition prevails in many places (Leighton, 1904). Such pollution causes a complete extermination of the fauna (and largely of the flora) and leaves the streams in such condition that restocking by either natural or artificial means is practically impossible.

Pollution by sewage, when the polluting material is of small percentage as compared with the pure water of the stream (as 200 to 1), causes little inconvenience to the animal life and is doubtless of some benefit because of the additional food material that is added (Forbes and Richardson, 1919: 146). But the streams seldom remain long in this innoxious condition, the sewage becoming more and more concentrated until the whole stream may be supersaturated with noxious substances, the amount of oxygen in saturation reduced, and the biota finally driven out or killed.

The Illinois River is one of the most striking examples of the effect of sewage pollution on the life of a stream. Under the direction of Dr. S. A. Forbes, studies of this river have been carried on for more than forty-two years (since 1877) and a mass of reliable data has been gathered. The opening of the Chicago Drainage Canal in 1890 produced most revolutionary changes in the life of the Illinois river, by the discharge into it of the sewage of Chicago as well as commercial wastes from this city and other places along the river (Forbes and Richardson, 1913, 1919). The effect of this sewage pollution has been to cause the animal life to be almost excluded from the upper parts of the river. That the polluted condition is creeping down stream is shown by comparisons of collections made in 1911 with those made in 1918. In the earlier years a foul-water fungus disappeared from the river near Starved Rock; in 1918 it was found at Henry and Lacon, 35 and 41 miles farther down the river (Forbes and Richardson, 1919:145). At the present time (1919) optimum conditions and a normal river fauna are not encountered until Peoria is reached, a distance of about 120 miles from the chief source of pollution at Lockport. Sewage from the towns and cities along the river also contribute to the general septic condition.

A striking example of the deadly effect of sewage pollution on the mussel life of a stream is given by Wilson and Clark (1912:34) in their study of the Kankakee River mussel fauna. "The DesPlaines River, which joins the Kankakee to form the Illinois River, is simply an immense sewer bringing down the Chicago sewage. Both rivers, but especially the DesPlaines, are full of the characteristic algae and other vegetation which grow in such waters, and the combination of a copious vegetation with the sewage has effectually killed off all the mussels in the vicinity. Not a single living specimen could be found in either river; but there were hundreds of dead shells along the banks, most of these old and well bleached, but still capable of identification." This statement, of course, applies only

to the lower part of the Kankakee River where the influence of the polluted DesPlaines has worked upstream for some distance. The Kankakee River for the most part is a highly productive stream with a high rate of dissolved oxygen, in fact, the water is supersaturated with this life-giving element.

In the Maumee River (Wilson and Clark:1912, 26, 28) shell beds were found which had probably been killed by the refuse from gas works near the junction of the St. Mary's and St. Joseph's rivers. "Spots of tar were found on dead mussels some distance below this point. The water was covered with an oily scum in places and a tarry odor was perceptible for several miles down the river." Lower down the river the mussels were showing the effect of increased pollution of the river by sewage.

The pollution is worst and usually the most deadly to animal life during periods of low water and in winter when the amount of water in the stream is small and the decomposing organic material has less water to deprive of its dissolved oxygen. During times of floods the putrescent material is also carried down the stream for many miles and contaminates areas not previously affected.

While all clean-water forms of animal life are more or less affected by sewage pollution, the decomposition of organic matter abstracting dissolved oxygen from the water and rendering it unsuitable for aquatic life, the fish, river mussels and crayfish are particularly affected, most fish being especially sensitive to contaminated water. Some fish (as the brook silversides, *Labidesthes sicculus*) are notably sensitive, while others (as the black bullhead, *Ameiurus melas*) will endure water that is badly polluted (Shelford, 1918:27; Wells, 1918:562-567). The young fish are relatively more sensitive than the adult fish. It is noteworthy that the more resistant species of fish are inhabitants of sluggish bodies of water, as ponds and shallow lakes, while the least resistant species live in running streams. It seems to be a question of the amount of oxygen necessary for the well being of the fish.

The ill effect of sewage pollution is most marked on the bottom of bodies of water, where a sludge is formed, often of great thickness (as much as ten feet in some instances), consisting of a mass of soft, black, sediment with a high content of organic matter, in which only a few organisms, normally inhabitants of polluted streams, can live (e.g., septic Protozoa and Rotifera, foul-water algae, and slime worms, Tubificidae). This effect on the bottom is perhaps the most serious phase of stream pollution because the septic condition of this area continues in operation long after the original source of contamination ceases to operate. This sludge formation renders the bottom unfit for clean-water life upon which many fish depend for food.

The effect of sewage pollution on the fish population of the upper Illinois River has been marked, many species, such as catfishes, red-horse,



buffalo, and sheepshead, which were formerly very common and taken in quantity by the fishermen several years ago, are now either wanting, or greatly reduced in numbers. Other fish, not bottom feeders, such as sunfishes, crappies, and the basses, are reported to be decreasing in recent years as polluted conditions are creeping down the river (Forbes and Richardson, 1913:544). It has been observed that fish entering a polluted stream from a clean-water tributary soon die if unable to return to clean water. The fauna of a polluted stream also becomes gradually of greater size as the distance from the source of pollution increases. This has been observed by Forbes and Richardson in the Illinois River, by Ortmann in the Allegheny River, and by the author in the Big Vermilion River. The time necessary for the recovery of the normal biota of such a stream will in most cases be of long duration and in the case of a stream polluted by wastes from mines and chemical manufacturies, there may never be a return to the original condition.

In New York State, the Genesee River, at Rochester, has afforded a striking example of stream pollution, of the effect of this pollution on certain animal life in the river, and of the return of this life when the amount of pollution has been largely reduced. This stream has been under observation by the writer for a period of twenty-seven years (1892 to 1919) and collections of the molluscan life have been made from time to time, both before the period of maximum pollution and since that time. The portion of the river studied lies below the lower falls north of the city, and about a quarter of a mile below the outfall of several trunk sewers, the sewage being discharged into the river in a crude condition. Refuse and other waste matter, both liquid and solid, also enter the stream from gas works, tanneries, and manufacturing plants above the lower falls.

Collections made in 1892, before pollution became notably apparent, included nine species of gastropod mollusks, three being water breathers and six air breathers. These species included:

*Musculium transversum*  
*Musculium partumeium*  
*Bythinia tentaculata*  
*Planorbis trivolvis*  
*Physa gyrina*

*Physa sayii*  
*Physa oneida*  
*Galba catascopium*  
*Galba caperata*

Individuals were notably abundant, thickly covering the rocks and the shore. In 1897, it was observed that the sewage was increasing in volume and pollution was becoming more noticable, the water appearing like very heavy, greasy dish water. The river was visited and examined at short intervals from 1898 to 1919. Each year it was noted that pollution was rapidly increasing. In 1907, the water-breathing mollusks, *Musculium* and *Bythinia*, had succumbed and none could be found. The air-breathers, *Galba*, *Planorbis*, and *Physa*, still held out, though

reduced in number of individuals. An examination made in 1910 failed to discover a single living mollusk of any species. Apparently the water had reached such a state of concentrated pollution that even the air-breathing mollusks, which normally come to the surface to take free air, could not adapt themselves to this unfavorable environment and were either killed or compelled to migrate down the river to a point where pollution was less deadly. During the following years, 1910 to 1913, the river was visited but no mollusks were found.

During the summer of 1912, G. C. Whipple, made a study of the effect of the sewage pollution on certain animal and vegetal life in the Genesee River (Fisher, 1913:179-200). This study was made when pollution was at its maximum and during the period when molluscan life had disappeared from the lower part of the river. The dissolved oxygen in the lower river, below the trunk line sewer, in July and August, when the temperature was high and the water low, varied from 5 to 41 per cent of saturation. The water at the bottom of the river almost always contained less oxygen than that at the surface. On one day in August, the percentage of saturation in a distance of three miles did not exceed 5 per cent from the surface to the bottom of the stream, which has a depth of about twenty-six feet. The number of bacteria per cc for this period was 1,650,000 near the source of pollution and but 67,000 per cc near the mouth of the river where the influence of the pure water from Lake Ontario increased the amount of dissolved oxygen.

In 1917, a large part of the city sewage was diverted to a disposal plant situated near the shore of Lake Ontario. Here an average of 32 million gallons of sewage are treated daily and the treated sewage is discharged into Lake Ontario in deep water at some distance from shore. It is at once apparent that when this large amount of sewage was discharged into the Genesee River in a crude condition, it could not but render the water totally unfit for animal life and a menace even to the inhabitants who visited the beautiful parks bordering both sides of the lower Genesee River.

The result of the diminution in the amount and character of the sewage discharged into the river has been that the molluscan fauna, as well as other forms of aquatic animal life, have returned and are rapidly taking possession of the favorable environments which were in use previous to the maximum period of pollution. Collections made in September, 1919, contained six species, two being water-breathers and four air-breathers.

*Musculium transversum*  
*Bythinia tentaculata*  
*Galba catascopium*

*Planorbis trivolvis*  
*Physa integra*  
*Physa oneida*

It will be noted that of the returned species, one is different (*Physa integra*), while four are missing, *Galba caperata*, *Physa gyrina*, *Physa sayii*, and *Musculium partumeium*. It frequently happens that when a fauna returns to a habitat from which it has been driven by unfavorable conditions, it is made up of a different aggregation of species (see Ortmann, 1909, for additional notes on this subject).

The Genesee River is a striking example of the history of a polluted stream and its effect on one group of animal life. Previous to the stage of greatest pollution there is a varied fauna of mollusks very numerous in individuals. In the course of eleven years the gill-bearing species are forced out and after a lapse of fourteen years all molluscan life ceases to live in this part of the river. Seven years later the greater amount of sewage is diverted to another outlet. Two years after this change the mollusks have returned in as great numbers as before the maximum stage of pollution. The significance of all this lies in the fact of the early return of this life and strikingly indicates that streams may become restocked with life in a short period after pollution has ceased to be of an unfavorable character, provided, of course, the bottom of the stream has not been made permanently untenable by the deposition of poisonous substances that cannot be washed away by ordinary river currents. It is quite probable that the large fall of water, some 60 feet in height, immediately above the sewage outlet, has had a marked effect in the return of these favorable conditions.

No additional data are at hand indicating the changes in a polluted stream after septic conditions have ceased or become greatly modified. It is probable that similar beneficial results would be obtained in other streams if the sewage was diverted or treated to remove the large amount of organic matter. In the case of a stream like the Salt Fork, the septic condition of which will be discussed in the following pages, it would probably not require a very long time to reduce the septic conditions if the sewage from Urbana and Champaign were properly treated. While the putrescible matter at present covers everything, in some places to a considerable depth, the high water during the spring would in several seasons remove a large part of this material, and if no additional matter was permitted to flow into the stream, the lapse of a few years would enable nature to bring the stream back to a normal, healthy condition, and make it a place to seek for recreation instead of a place to avoid on account of its filth, as at present.

#### SEWAGE POLLUTION IN THE SALT FORK

The sewage and other wastes of the Twin Cities of Urbana and Champaign are discharged into the waters of the Salt Fork by separate systems, that of Urbana emptying into the Boneyard near the Big Four shops, while



the sewer outlet of the Champaign system is situated on the Salt Fork about a mile below the Urbana outlet. There are two systems for each city, one for domestic wastes and the other for the care of storm water, the sanitary sewage. Septic tanks were installed with the systems, about the year 1894, to reduce the amount of putrescible matter, but at the present time the sewage receives little treatment and practically enters the Salt Fork in a crude condition.\* The population in 1914 was estimated to be 13,750 for Champaign, and 9,252 for Urbana, or a total population of about 23,000 for the Twin Cities. At the present time, 1920, six years later, the increase has probably brought the total up to nearly 30,000. The sewage system, therefore, provides disposal for this population, and is all discharged into the waters of the Salt Fork. It is estimated by G. C. Habermeyer, that the total flow of sewage from the Urbana plant is about 500,000 gallons per day and from the Champaign plant about 1,000,000 gallons per day.\*\*

The flow of the Salt Fork below the Champaign sewage disposal plant is 3,000,000 gallons per day. These figures indicate that the sewage forms one-half of the total water flowing down the Salt Fork. These data were taken in October, when the stream was low, and may be a trifle too high for those periods when there is a rise of water following a period of rainy weather. During a greater part of the year, however, the water is low and these figures will be approximately correct. The fresh water added to the sewage is derived from the stream north of Urbana which contributes 250,000 gallons per day, and the Boneyard, which adds 1,500,000 gallons per day, about two-thirds being clear water. "In October, 1917, the flow in the Boneyard below the Urbana tank was about one-third sewage and probably contained considerable other waste and sewage discharged above the Urbana sewage outlet. The flow in Salt Fork below the Champaign sewer outlet was probably one-half sewage."

H. E. Babbitt,\*\*\* thus describes the condition at the Champaign disposal plant at this date. "The appearance of the effluent from the Champaign septic tank is that of fresh sewage, having the typical color of sewage, and carrying fecal matter and paper. The appearance of the Salt Fork at the point of entrance of the sewage from the tank is good. It is about twenty

\* New septic tanks have been installed at the Champaign sewage disposal plant on Salt Fork and a portion of the sewage is well treated before it enters the canal.

\*\* Data for the sewage conditions, stream flow, chemical analyses, etc., of the Salt Fork are taken from an unpublished report of G. C. Habermeyer (assisted by S. D. Kirkpatrick, assistant chemist, and J. F. Schellbach, engineer) made for the State Water Survey Division of the Department of Registration and Education, of Illinois, and here used by permission of the late Chief of the Division, Dr. Edward Bartow.

\*\*\* From unpublished Report on the Champaign-Urbana Water Works System, prepared June 23, 1914. Extracts here published by permission of Edward Bartow.



feet wide, fifteen to eighteen inches deep, clear, colorless, and odorless. The stage of water at the time of inspection was low. No septic action was present except in the open ditch through which the sewage flows from the tank into the stream. There is a large sludge bank in the stream immediately below the outlet and a most obnoxious odor." Effluent from the Urbana tank appeared as typical fresh sewage, but was not representative of the ordinary effluent as the tank had been cleaned only the day previous to the visit (page 9).

The stream known under the name of the "Boneyard" carries both waste and sewage. This stream is about three and a half miles in length and rises about half a mile beyond the northern limits of the City of Champaign. The stream flows southward to near Third and Green streets, where it abruptly turns eastward, emptying into the Salt Fork near the Big Four shops in Urbana. This stream has a drainage area of about eight and a half square miles. Sewage enters the Boneyard near Goodwin Avenue and at the old high school on Stoughten Street, Urbana. Water bearing wastes, presumably from business houses near by, enters the stream north of Main Street. The banks close to the water line near Main Street culvert are slimy and green (data from G. C. Habermeyer, 1918).

The Boneyard is subject to great fluctuations of water level, due to the severe storms of spring and summer when heavy rains occur. At such times a rise of three or four feet in a few hours is not unusual and the waters overflow all adjacent low land. At one time (reported very bad in 1915) chemical wastes in the form of oil and tar were discharged into the stream from the gas works of the Champaign Street Railway, Gas and Electric Company, situated at the corner of Fifth and Hill streets, Champaign, east of the Illinois Central tracks. The oil at one period extended the entire length of the Boneyard, covering lawns, when the water was high, with an unsightly layer of heavy oil. The shores and bottom of the stream in many places were covered with tar, which has not subsequently been removed and also cannot be removed by the natural flow of water, but must be artificially taken from the stream bed.\*

The oil discharged from the gas works, as well as from some other points along the Boneyard, is absolutely inimical to any life in the stream. The tar, if carried down stream, finally settles to the bottom and unless artificially removed, will remain there and render the stream unfit for bottom inhabiting life of any kind. Fortunately, such pollution is confined to the upper part of the Boneyard. Waters charged with sewage may become purified in a year or two after pollution ceases, but they will seldom or never recover from chemical pollution such as is produced by tar

\* From Ralph Hilscher, Report on Contamination of the Boneyard in Champaign by Gas House Wastes August 28, 1915. Here published by permission of Edward Bartow.

and similar wastes. Ortmann's work on the rivers of western Pennsylvania clearly indicate the baneful results of such pollution (Ortmann, 1909).

The Boneyard is apparently now barren of all clean water life. Frequent examinations made during 1918 failed to supply any life of this character. Fresh water pulmonate mollusks, and *Cambarus* and other smaller Crustacea were once abundant, but appear to be wanting at the present time. A large snapping turtle was observed in the Boneyard near Lincoln Avenue, in 1918. The ditched portion of Salt Fork above Urbana, is a clean water stream, filled with aquatic life, which abruptly terminates at the junction of this stream with the Boneyard, with its load of sewage from Urbana. From here to a point fourteen miles below Urbana not a living mussel was found, and no air breathing snails were observed, except in one instance, believed to have been introduced from a near-by portion of the old river bed, which still retains clean water life, above St. Joseph, a distance of ten miles below Urbana. The large number of empty valves and paired shells of the river mussels below St. Joseph indicate an environment that has become, more or less recently, inimical to these creatures. Crayfish were also absent from the same area.

Habermeyer's report of Salt Fork, October 1, 1917, describes conditions as follows: "The stream below the Champaign outlet to the north line of section 10, one and a half miles below the outlet, was in very foul condition. At the east line of section 11, four miles below the Champaign sewer outlet, the stream appeared to be quite clear and there was no offensive odor noticeable. At the outlet of the west branch of Salt Fork, the water was clearer than that in the north branch (Spoon River). A resident near the junction of the two branches stated that at times when the creek flow increased, foul matter was washed down from above and there was considerable odor in the vicinity for a day or two."

The dredging of a new channel has been responsible for the water being clearer at times in Salt Fork than in Spoon River, providing a sand bottom which is hard and resistant and has not yet silted up to any degree. Spoon River has a mud bottom and the waters are turbid a large part of the time. In a photograph of the Salt Fork taken some eight miles below Urbana (two miles northwest of St. Joseph), the water was so clear that the ripple marks on the sandy bottom may be distinctly seen in the picture (Fig. 45) yet the stream at this point was totally barren of clean water life and the water was laden with masses of decomposing matter, made up of foul water algae and Protozoa, and the bottom was filled with slime worms (*Limnodrilus*). Below the junction of these two branches, bottom conditions are still very bad, and clean water life does not appear for a distance of several miles, as has already been shown.

The people mentioned in the report were interviewed in 1918. They reported that no trouble was experienced during periods of low water, but

that after rains, when the stream rapidly rose, putrescible matter was washed down stream, cast on shore, and the odor was then very bad. This lasted until the water subsided. In the fall of 1920, the same people were again interviewed and conditions were reported to be much worse than previously, the unusually low stage of the water causing the putrescible matter to decay on the exposed sand bars in the river, from which some odor was noticed.

Stream measurements of the velocity of the current were made by the Water Survey at several points along the Salt Fork. These were made by Habermeyer on October 1, 1917, when the water was low in the stream. All data given in feet.

TABLE IX. MOUTH OF THE BONEYARD

	1	2	3
Distance from east bank.....			
Depth of water.....	0.6	0.7	0.4
Flow per hour.....	4608	4500	4320
Salt Fork, Four Miles below Champaign Sewer Outlet			
Distance from bank.....	2.9	2.4	1.8
Flow per hour.....	3888	4320	4212

These measurements indicate a very slow current, from about one half to nearly a mile an hour. At high water the rate of flow is undoubtedly several times as great. This slow rate of flow would cause much of the heavy matter in the sewage to be precipitated to the bottom and form sludge banks, and this has occurred at many places below both the Urbana and Champaign outlets. High water and more rapid current probably moves some of this sludge farther down stream, also carrying the fresh sewage farther down at such times. A recent examination made at very low water indicates that this has been the case, for hundreds of bars were observed out of water, each covered with a sludge formation of greater or less size.

Analyses of water from various places in the Salt Fork and tributary streams have been made by the Water Survey. The two tables that follow, taken from Habermeyer's report, indicate some of the conditions of the upper waters of Salt Fork (Tables X and XI).

In Table X the low percentage of dissolved oxygen (saturation) in the ditched stream above Lincoln Avenue is noteworthy as compared with the larger amount at Cunningham Avenue. At both localities, however, the water is relatively pure, there being little or no pollution. The sample from a mile and a quarter below the champaign outlet is striking because of the total absence of oxygen. The sudden rise in saturation at four and eight miles is also notable, and indicates that at these points on this date little decomposition was taking place. The sample from Salt Fork near Spoon River shows a marked fall in the amount of dissolved oxygen,



TABLE X. BACTERIOLOGICAL EXAMINATION, RELATIVE STABILITY, AND DISSOLVED OXYGEN IN SAMPLES FROM BONEYARD AND SALT FORK

Laboratory number	Total no. of bacteria per c c		Gas forming organisms in						Dissolved oxygen		Relative stability in percent	Temperature water F	Locality
	On gelatin 20°C	On agar 37°C	0.1	.01	.001	.0001	.000001	.0000001	p.p.m.	Percent of saturation			
38173	280	4,600	...	...	...	...	...	...	5.17	55.5	84	...	West of Lincoln Ave.
38174	1,400	2,220	*	...	...	...	...	...	7.75	84.5	84	68	Cunningham Avenue
38175	580,000	650,000	*	*	*	*	...	...	0.00	00.0	21	71	1¼ miles below Cham-paign sewer
38176	70,000	50,000	*	*	*	...	...	...	6.10	66.7	84	...	4 miles below Cham-paign sewer
38177	32,000	12,000	*	*	...	...	...	...	8.05	89.7	84	70	8 miles below Cham-paign sewer
38178	2,700	30,000	*	*	*	...	...	...	5.07	54.2	84	67	Mouth of Spoon River
38179	40,000	20,000	...	...	...	...	...	...	6.80	68.5	21	61	Up Spoon River
38180	600,000	500,000	*	*	*	*	...	...	2.45*	25.6*	21	64	Urbana sewage out-let
38181	81,000	95,000	*	...	...	...	...	...	1.00	10.7	11	...	Mouth of Boneyard

\* Samples of dissolved oxygen and relative stability taken a short distance above number 38180.



TABLE XI. CHEMICAL ANALYSES OF SAMPLES FROM THE BONEYARD AND SALT FORK. PARTS PER MILLION

Laboratory number	Residue on evaporation		Loss on ignition. Dissolved residue	Chlorine in Chlorides	Oxygen consumed		Ammonia nitrogen	Albuminoid nitrogen		Nitrate Nitrogen	Nitrite Nitrogen	Alkalinity	Locality
	Total	Dissolved			Total	Dissolved		Total	Dissolved				
38173	455	365	170	4	4.6	4.6	.112	.240	.240	.72	.025	252	West of Lincoln Ave.
38174	580	575	190	13	4.0	4.0	.048	.144	.240	.64	.020	240	Cunningham Ave.
38175	745	645	280	62	16.0	14.0	18.000	3.200	2.000	.20	.000	410	1¼ miles below Cham- paign sewer
38176	615	600	250	51	11.2	11.0	14.800	.720	.680	.48	.250	348	4 miles below Cham- paign sewer
38177	605	590	245	56	12.8	11.2	7.000	.752	.640	2.00	.300	338	8 miles below Cham- paign sewer
38178	630	585	245	59	10.0	9.2	23.000	.720	.480	2.20	.250	356	Mouth of Spoon River
38179	400	380	160	6	7.8	7.0	.080	.296	.360	.40	.002	248	Up Spoon River
38180	830	675	320	56	68.8	26.0	19.200	4.400	2.080	.48	.000	464	Urbana sewage outlet
38181	645	580	265	63	36.4	15.2	6.400	2.400	1.440	.36	.000	376	Mouth of Boneyard
38182	1460	825	360	85	38.8	31.2	32.000	6.400	1.600	.56	.000	482	Champaign sewage at manhole close to Ur- bana sewage tank.

which coincides with the absence of mollusks and crayfish from this part of the stream. The rise of the oxygen content 200 feet upstream in Spoon River shows the effect of the cleaner water, and this also coincides with the presence of clean water life in this part of Spoon River. The lower temperatures were probably responsible for the rise in oxygen content at the stations four and eight miles below Urbana. In the summer months, during low water and high temperature conditions, the percentage would probably be much lower. This difference was noted by Forbes and Richardson in their study of the Illinois River. The percentages of dissolved oxygen are relatively higher in these two stations of the Salt Fork, four and eight miles from the source of pollution, than in the Illinois River at Starved Rock, Hennepin, and Chillicothe, where samples taken in October showed smaller percentages, though many miles from the chief source of pollution at Lockport (Forbes and Richardson, 1913:565).

The rise and fall in the number of bacteria and the presence of many gas-forming organisms in the Salt Fork is well shown in the table. The sudden rise from Cunningham Avenue to the point one and a quarter miles below the Champaign sewer outlet is very striking and indicates in a graphic manner the difference between clean water and that heavily polluted by sewage wastes. The high number 200 feet up from the mouth of Spoon River indicates that there is some pollution in this stream, although not far above this point living mollusks (*Naiades*) were found in abundance.

In Table XI, the relative high amounts of albuminoid nitrogen, as well as ammonia nitrogen, supplied by the sewage material, in contrast with the small amounts in the purer water of the stream, are strikingly shown. All of these agencies are inimical to clean water life, especially fish, mussels, and crayfish, which by their relative abundance or absence, indicate in a most satisfactory manner the quality of the environment, and its fitness for the well-being of its inhabitants.

The sewage in the Salt Fork has greatly increased in recent years, following the increase in population, and, as in the case of the sewage from Chicago in the Illinois River, the polluted condition is gradually creeping down the stream below St. Joseph, changing the pure water inhabitants to those that can live under septic conditions. As no collections were made during previous years from the stream below St. Joseph it is not now possible to make comparisons of the present with previous conditions. Such lists as have been available have not indicated precisely the location from which they were collected (as in the neighborhood of St. Joseph, which might mean in the Salt Fork or in Spoon River) and they cannot be used for this reason. The value of exact local lists is emphasized in studies of this kind, showing that strictly technical (or pure science) information is often of the greatest value in the study of economic problems.

## RECENT EXAMINATION OF THE POLLUTED PORTION OF SALT FORK

## Figures 21, 36 to 45

During the fall, winter, and spring of 1919 and 1920 Salt Fork was carefully examined from Urbana to St. Joseph. All parts of the stream were searched for macroscopic life and samples of the bottom and of the water were taken for microscopic study, to determine the character and abundance of the foul-water organisms present. Examinations were made during the months of May, September, October, November, and December.

During the spring months the water is so high in the stream that collections can not be made and examination of the water is difficult. The great volume of water, laden with both sewage and silt, is of a dark lead color and polluted conditions are not apparent, although some putrescent matter was observed on several occasions. In the fall months conditions are much more favorable for critical examination, the water being so low that one may wade over any part of the stream. It is at this time, which extends from July through the fall and winter to the rainy period in March or April, that the polluted conditions are very apparent and the most satisfactory studies can be made. The general conditions of the stream at this period are summarized below.

The water in the Boneyard near the Big Four shops, below the Urbana sewage outlet is usually shallow, from a foot or less to two feet in places. The bottom is a mass of sludge with putrescent material covering all objects in the water and floating down the stream, which has an estimated flow of about half a mile an hour. Several large sludge banks are exposed and the odor is usually nauseating (Fig. 39). At the junction of the Boneyard with the Salt Fork the water varies from six inches to a foot in depth, there are several sludge banks and the putrescent matter covers all objects and lines the shores to a height of several feet, indicating former high water marks (Fig. 36). Samples of the sludge and green putrescent material from one of these sludge banks were examined by Professors Smith and Transeau and the following algae, Protozoa and other animals observed:

## Blue-green algae

- Pediastrum simplex*, common.
- Senedesmus abundans*, rare.
- Phormidium inundatum*, abundant.
- Diatoms
- Navicula cryptocephala*, common.
- Synedea pulchella*, not common.

## Animals

- Paramoecium, not common.
- Euglena geniculata*, very abundant.
- Limnodrilus* (sludge worm), very abundant.
- Tubifex* (sludge worm), one specimen.
- Nematode worms, several.

Ciliate Protozoa were numerous, including *Colpodium* and a few hypotrichous and peritrichous species.



At the junction of the Boneyard with the Salt Fork the waters of the two streams usually formed two distinct bands, the clear water of the latter on the left or north bank and the murky, sewage-laden water of the Boneyard on the right or south bank, the line in the center of the stream dividing the two waters being clearly marked. (Fig. 21). The waters of these two streams do not fully mingle until they have flowed a distance of several hundred yards. All the way down the Salt Fork, however, as far as the first bridge, the right side is more discolored than the left side, indicating that the sewage-laden waters of the Boneyard and Champaign outlet flow mostly on this side of the stream.

At the Champaign sewage outlet, about half a mile below the Boneyard, there is usually a good flow of water from the discharge pipe into an open ditch, which empties into the Salt Fork a short distance away. At the point of entrance of the open ditch, the chocolate-colored water of the Champaign sewage is clearly marked as a dark band extending around the upstream end of a large sludge bank, similar to the one described in Habermeyer's report in 1917 (Fig. 41). Some fecal matter is generally present. The water in the Salt Fork at this point is usually less than a foot deep and the bottom is made up of a soft sludge which covers everything in the water. The odor is very bad, almost nauseating.

Below the Champaign outlet the stream is in very foul condition, as noted in Habermeyer's report. From the outlet to the first bridge, more than a mile down stream, the water is less than a foot deep, in most places but a few inches, and the bottom has much sludge, and putrescent matter covers every object in the water, as well as the shores and all objects on the shores to a height of several feet, indicating former stream levels. Fecal matter, in dark brown masses, as well as partly decomposed organic matter colored green by the presence of blue-green algae and the protozoan *Euglena*, are usually floating down the stream. The bottom substratum is of sand and gravel, and over this sludge banks have been formed of greater or less thickness. Bars of sand and gravel occur at irregular intervals and are covered with masses of putrescent matter forming long, alternating streaks of black and green. An oily scum resembling petroleum covers the surface in many places, and the bottom, when disturbed, emits an oily substance which spreads over the surface as an oily scum. This may represent some gas house wastes as well as heavy oil from other places along the Boneyard. The odor in this section of the stream is almost overpowering in many places, being distinctly a privy smell. In one place the observer was compelled to leave the vicinity of the stream, the odor was so strongly nauseating. In places, bubbles of gas may be seen to break at the surface from submerged sludge banks.

Samples of the bottom sludge and putrescent matter floating in the water were collected just above the bridge, about a mile and a quarter



below the Champaign outlet. Algae and animal life were noted, but not as abundantly as in the sludge bank at the junction of the Salt Fork and Bone-yard (Fig. 21).

Animals	Blue-green algae
<i>Euglena geniculata</i> , very few.	<i>Phormidium inundatum</i> , abundant.
Paramoecium, one specimen.	Diatoms
Vorticella, very few.	<i>Navicula salinarum</i> , abundant.

The scarcity of microscopic life and the total absence of clean-water life is paralleled by the chemical condition of the water at this station, where the examination of samples showed a total absence of dissolved oxygen and the presence of multitudes of bacteria and gas-forming organisms (see Tables X, XI).

From the first iron bridge to the Brownfield woods bridge, a distance of about a mile and a quarter, the stream is very shallow, less than a foot in depth on the average, the water grayish with a sloppy appearance, and the odor foul in places, though not as nauseating as below the first bridge. Putrescent masses of soft, grayish-black or greenish matter, ranging in size from a penny to a platter, may be seen floating down stream, held together by algal strands. Brown masses observed on shore resembled human excrement. The oily appearance of the surface of the water continues and oily matter ascends when the bottom is disturbed.

From the Brownfield bridge to the third (farmer's) bridge, a distance of about three-quarters of a mile, the conditions are the same as above this bridge (Fig. 38). Between the third bridge and the Cottonwoods road bridge, a distance of about a mile, the water is very shallow, scarcely exceeding six-inches in depth, with gravel or sand bottom. Sludge bars, of sand mixed with organic matter, are frequent, in many places occupying more than half the width of the stream, the channel, a few inches to a foot in depth, meandering over the bottom between these bars (Fig. 40).

These bars presented a striking appearance, the stones and sand being black from the decomposing organic matter, and the foul water algae being arranged in long streaks, presenting in combination a striped green and black design. The green algae is here very abundant, floating in the stream or covering the shores. In places the encrusting material on the shore margins is bright yellow. Everywhere along the stream the exposed surface of the bottom is black from the decomposing organic matter, which covers all objects and has been baked hard by the hot summer's sun. The vegetation bordering the shore also shows the effect of sewage action, being either black in color or having the dried pieces of polluted material attached to the lower part of the plants. The same conditions prevail from the Cottonwoods road to the Mayview road, a distance of about two miles.

Collections of materials made just below the third farmer's bridge, about three and a half miles below the Champaign outlet, contained the following organisms:

Blue-green algae	Animals
<i>Phormidium inundatum</i> , abundant.	Flagellate Protozoa, very minute.
Diatoms	<i>Euglena geniculata</i> , very abundant.
<i>Navicula salinarum</i> , abundant.	Many in stage of encystment.
	<i>Dineutes assimilis</i> , very abundant.
	On the surface of the water.

Collections at the Cottonwoods bridge (Fig. 42) contained a larger variety of animal life, which was rather meagerly represented above this bridge. This place is on the east line of section 11, about four miles below the Champaign outlet. The bottom here is of fine sand and mud.

Blue-green algae	Animals
<i>Phormidium inundatum</i> , abundant.	<i>Euglena geniculata</i> , very abundant.
Diatoms	Rotifer, illoricate, one specimen.
<i>Navicula salinarum</i> , abundant.	Limnodrilus, two specimens.
	<i>Dineutes assimilis</i> , a few examples.

Mussel shells or other mollusks were entirely absent in a living state and their shells were notably rare. About three quarters of a mile below the first bridge east of Urbana, a half valve of *Lampsilis luteola* was found on a sand bar (Fig. 37). Near the Brownfield woods bridge many broken pieces of mussel shells, as well as a few mutilated half valves, were observed. At a farmer's bridge half a mile below this bridge several broken valves of *Lampsilis luteola* and *Anodonta grandis* were collected, (Fig. 38) and from this point down stream to the Cottonwoods road bridge detached valves or broken pieces of shell were more or less common. From observations of this and other parts of the stream it seems evident that these mutilated shells were washed from the spoil banks on either side or from the bed of the old stream channel where it crosses the canal. At the junction of the Boneyard with the Salt Fork a layer of these shells was observed in the bank, about eighteen inches above the water line (the water being low), in a position that indicated the old bed of the Salt Fork before the canal was excavated. High water would wash this material way and provide the odd valves of mussels observed in different parts of this stream.

Below Mayview road bridge the conditions are much the same as in the neighborhood of the Cottonwoods bridge. The bottom is of sand and gravel, with some mud bordering the shore. The water is from a few inches to a foot in depth, the channel meandering among a continuous series of sand bars. The sand is ripple-marked in places and streaked with bands of dark green algae, with yellowish algae in spots. The surface of the flowing portion of the stream is thickly covered with patches of dark

green putrescent matter, measuring in size from a peanut to a dish pan. Some of these masses are brownish, where the algae and Protozoa have not completely taken possession of them.

A large amount of oily scum may be observed on the surface and when disturbed the bottom emits quantities of oily matter, as is the case higher up the stream. On exposed bars and along shore the algae and putrescent matter have dried and caked, forming a pavement-like layer. The water is clearer here than in the portion of the stream previously examined, but no clean water life could be found; mussels, crayfish, and insects were entirely absent.

Samples of the bottom from the stream about 300 feet east of the Mayview road bridge, about six miles below the Champaign outlet were examined. The following life was present:

Blue-green algae	Animals
<i>Pediastrum simplex</i> , rare.	Ciliata, minute, abundant.
<i>Phormidium inundatum</i> , common.	Colpodium, several.
Diatoms	<i>Euglena geniculata</i> , very abundant.
<i>Navicula salinarum</i> , abundant.	Limnodrilus, common.
<i>Fragilaria capucina</i> , abundant.	Nematode worms, minute, abundant.

About a mile and a half below this locality additional samples were taken for examination. Conditions are similar but the water is not as clear, holding more sediment in suspension.

Blue-green algae	Animals
<i>Pediastrum simplex</i> , rare.	Ciliata, minute, abundant.
<i>Phormidium inundatum</i> , abundant.	Paramoecium, several.
Diatoms	<i>Euglena geniculata</i> , abundant.
<i>Fragilaria capucina</i> , abundant.	Limnodrilus, about a dozen.
	Nematode worms, minute, many.

At the last north and south farmer's bridge, the canal makes a wide sweep, in a southeasterly direction (Fig. 43) leaving the old stream bed to the west of the new channel, in the form of an 'ox-bow' almost half a mile in length, which, during the greater part of the year, forms a large elongated pond, that drains into Salt Fork canal by means of a small outlet at the south end which turns abruptly northeastward as it empties into the canal. At the time examined, the bed of this old stream was almost dry, following a period of very dry weather, and the fauna had retired to several small, shallow, muddy pools which remained in the deeper parts of the stream bed. An examination of these pools disclosed a number of bull-heads (*Ameiurus melas*), many dragonfly larvae (*Libellula pulchella*), and a few mollusks (*Planorbis trivolvis*, *Physa gyrina*, and *Musculium transversum*).



It seems evident that this portion of the old stream forms a reservoir from which certain species of mollusks, as well as fish, are carried, or voluntarily migrate, through the outlet into Salt Fork. By this means only can the presence of these animals in the polluted water be accounted for, because none have been seen either above or far below the drain from the old stream channel. The specimens of *Planorbis trivolvis*, that have been observed in the Salt Fork canal below the east and west road bridge, were probably derived from this source.

Specimens of *Planorbis trivolvis* have been observed in the Salt Fork canal which probably came from this source. Near this locality a school of about fifty fingerling bullheads was observed on May 29, in a small part of the stream where a rather deep pool had developed. They were making frantic efforts to get out of the pool but the surrounding water was too shallow. The low water and general polluted condition of the stream evidently provided a very unfavorable environment. The source from which these fish came was quite likely the old cut off portion of the original Salt Fork from which place they had been carried or had voluntarily migrated, when the water was higher from the April rains.

From the east and west road bridge (Fig. 45) to the first farmer's bridge, a distance of about three-quarters of a mile, the conditions are the same as in the preceding portion of the canal. The water is clear but no living mollusks or other animals could be found. A half valve of *Anodonta grandis*, badly weathered, and a few bleached valves of *Sphaerium solidulum*, were the only evidences of molluscan life. These had evidently been washed from the old stream bed at some point where it was exposed by erosion in the canal walls. The same algae as previously observed was floating down the stream in large green patches. Samples of these green particles were examined by Professor Smith and found to contain such animals as *Euglena geniculata*, Paramoecium, and numerous ciliate Protozoa, mostly inhabitants of polluted water.

From the next farmer's bridge to the eastward turn of the stream the bottom conditions were also similar, except that the surface of the water was covered with an oily scum. Groups of greater or less size of gyrenid beetles (*Dineutes assimilis*) were seen at different places down stream for a mile or more. A single empty shell of *Planorbis trivolvis* was observed on the shore of the west bank below this bridge. No living clams were seen, nor any mutilated valves.

From the eastward turn of the stream to the mouth of Spoon River, the canal is in bad condition, the water being dirty and oily, with numerous bubbles of gas rising constantly from the bottom, which also gave off quantities of oily scum when disturbed (Fig. 44). The water is shallow and conditions as already described for the stream higher up. Green



putrescent matter is not quite as abundant as higher up in the canal and the odor is not as bad.

Samples were collected from a point about a mile above the junction of Salt Fork with the Spoon River. Organisms were fewer in both species and individuals.

Blue-green algae	Animals
<i>Phormidium inundatum</i> , common.	Ciliata, abundant.
Diatoms	<i>Euglena geniculata</i> .
<i>Synedra pulchella</i> , abundant.	Limnodrilus, a few individuals.
<i>Fragilaria capucina</i> , abundant.	

Below the mouth of Spoon River conditions are also bad. Where the current is strong, sand bars have been formed which cover the black mud beneath. Everywhere, except in the channel where it is sandy, the bottom is of soft mud, eight to fifteen inches deep, filled with ill-smelling gasses. Sewage conditions here are bad, the water having a foul smell. When wading in the water, the disturbed mud, which is black and oozy, constantly gives off bubbles of gasses that rise to the surface and break. This condition is uniform for the entire stretch of stream bed examined, about a third of a mile, from near the mouth of Spoon River to the middle of the big bend above St. Joseph. The surface of the water is usually covered with a film of oil resembling petroleum.

No living mussels could be found in this area. A single valve of *Amblyma undulata* was seen near the mouth of Spoon River which was probably brought to its resting place from Spoon River during a period of flood. It is noteworthy that while no mussels or gill-bearing snails were observed in this part of Salt Fork, several species of fresh water pulmonates were seen in considerable numbers, indicating that here, as elsewhere, the pulmonates are able to live in water which is totally unfit for mussels and gill-bearing mollusks.

Examples of the bottom sediments and green masses floating in the water were taken from the stream about a hundred feet below the mouth of Spoon River. Algae was plentiful and included *Phormidium inundatum*, a blue-green species, in abundance. Two species of diatoms, *Navicula salinarum* and *Fragilaria capucina*, were also present. Of animals, Limnodrilus was well represented, but *Euglena geniculata* was not common, and ciliate Protozoa were much less numerous than in samples taken from stations higher up in the stream. Salt Fork here shows the influence of the added cleaner water from Spoon River.

At the mouth of Spoon River a bar has been formed, by natural or artificial agencies, which, except for a space about four feet wide, holds back the waters of that stream (Fig. 16). An examination was made of Spoon River about 400 feet above this bar. Here five species of mussels

were found, in more or less abundance, and insects were also abundant. The water is low, two or three feet deep in the channel in the fall and the bottom is very muddy. A very small amount of green algae was noted on the surface, evidently brought up from Salt Fork. The mussels collected included:

*Lasmigona complanata*

*Amblesma undulata*

*Carunculina parva*

*Lampsilis luteola*

*Eurynia lienosa*

A water boatman (*Corixa*, near *burmeisteri*) was very abundant, especially in the nymph stage, as were also numerous gyrinid beetles (*Dineutes assimilis*). Though the water was low, men were observed fishing for bullheads in this part of Spoon River. The contrast between this stream, with its abundance of clean water life, and the adjacent parts of Salt Fork, which is utterly devoid of clean water life, strikingly indicates the harmful effects of sewage pollution on the fauna of our streams.

Samples of the green matter floating on the water of the Spoon River were examined and found to contain *Euglena geniculata*, common, ciliate Protozoa, many. These masses seem to be made up almost entirely of these animals and low plants, of which three species were noted: *Phormidium inundatum* alga; *Navicula salinarum* and *Fragilaria capucina*, diatoms. A single pupa of *Chironomus decorus* was found at this place.

For a distance of several miles below St. Joseph unfavorable conditions seem to prevail, no living mussels being found for a distance of over four miles, and here they occur rarely. Living mussels are not found in any number for a distance of over five miles below St. Joseph. These animals are not abundant in species and individuals until a distance of twenty miles has been traversed below Urbana. Conditions for a distance of two miles below St. Joseph are similar to those described for the area just below Spoon River, the bottom consisting of black mud from which bubbles of ill-smelling gas rise when the bottom is disturbed. Below this point conditions begin to improve, though very gradually.

That conditions along the polluted portion of Salt Fork are often, if not always, highly objectionable was evidenced from conversations with farmers living near the stream. One farmer, who had built a small house within a few hundred feet of the stream, stated that the "stench was at times almost unbearable" and that people living half a mile away were strongly conscious of the odor. This was about five miles down the stream from Urbana. A gentleman driving along the road which parallels the Salt Fork east of Cottonwoods road, stated that the odor on September 10 was very obnoxious. People living a mile south and north of the stream do not suffer from these odors.

## SUMMARY OF SALT FORK CONDITIONS

It has been shown in the previous pages that the sewage and other wastes that drain into the Salt Fork from the Twin Cities have driven out or killed all clean water life from the junction of the Boneyard with Salt Fork to a point about four miles below St. Joseph, or fourteen miles below Urbana. At this point a few living mussels are found and also a few crayfish. One must pass down the stream for a distance of twenty miles before encountering a normal river fauna, comparable to that found in Spoon River at a point less than a mile above the junction of that stream with Salt Fork. The abundance of clean-water life in Spoon River is in marked contrast with the total absence of this kind of life in Salt Fork, which normally would have, in suitable habitats, a similar fauna in the barren stretch of ten miles between the two localities compared. No better example is known of the total annihilation of a fauna from so great a distance as the result of polluted conditions.

Foul water algae and Protozoa, as well as some other animal life (slime worms) characteristic of polluted water, are abundant in that portion of the stream devoid of clean water life. The same relative conditions were observed by Forbes and Richardson in their study of the Illinois River.

Fish, especially young fish, have been made an index to the degree of pollution of streams. It would seem from observations made during the course of the present study, as well as from other occasions and in other places, that bottom-inhabiting animals, such as river mussels and crayfish, provide a better index for this purpose. Fish are able to migrate easily and swiftly from an unfavorable to a more favorable environment, but these more sedentary animals, especially the mussels, cannot change their environment so easily and must either adapt themselves to the more unfavorable conditions or perish. For example, young bullheads were observed in Salt Fork about three miles above St. Joseph in the spring when the water was comparatively high. But no mussels or crayfish have been seen within five miles of this point. This indicates clearly that fish are more flexible in this matter than the mussels and crayfish, which are not as mobile. Ortmann (1909:93-94) believes that crayfish are slightly more resistant than mussels to polluted conditions, and as scavengers (they have been observed eating dead mussels) they could naturally withstand a limited degree of unfavorable environment. Observations made on the Salt Fork, however, indicate that the two groups appear at about the same time.

Forbes and Richardson (1913:498) distinguish three stages of impurity of streams, which may apply equally well to either the stream itself or to the organisms living in the stream. These terms are "given in the order of diminishing impurity, namely, (1) septic or saprobic, (2) polluted or

pollutional, and (3) contaminated or contaminate; and to these we will add 'clean-water' to indicate the conditions and organisms substantially equivalent to those of the natural, uncontaminated stream."

Judging Salt Fork by these standards of impurity, we would say that from the Urbana sewage outlet to the first bridge below the Champaign sewer outlet, a distance of about two miles, the stream is in a septic condition. From this point to about two miles below St. Joseph it is polluted. From this region to Homer Park, below the dam, it is contaminated. Below the dam there is probably some contamination at times, but the fauna is a clean water one and the stream would be classed as a clean water stream, being unmodified by sewage conditions. The lower part of Salt Fork near Middle Fork, and Middle Fork and the Big Vermilion as far as Danville are clean-water streams with a large and varied fauna of mussels, crayfish, and insect larvae. Below Danville there is sewage pollution, and conditions are again unfavorable.



## SUMMARY AND CONCLUSIONS

The mussel fauna of the Big Vermilion River consists of at least 35 species and varieties. Ten species of small pelecypods and 15 species of gastropods also occur, making a total molluscan fauna of 60 species and varieties occurring in a distance of upwards of 50 miles. The mussel fauna of this stream compares well with that of two other Illinois streams of comparable size, the Sangamon, 150 miles long, with 25 species, and the Kankakee, 300 miles long, with 48 species. The total length of the Big Vermilion River is 90 miles, with 35 species. Seventeen species of Naiades occur in the Big Vermilion River that have not been found in the Sangamon River, while five species have been collected from the Sangamon that have not yet been detected in the Big Vermilion. The former stream belongs to the Mississippi drainage while the latter is a part of the Wabash drainage.

In the Big Vermilion it was noted that there was a progressive increase in number of species as the distance down stream increased, the headwaters containing but few species, which are usually smaller than the same species from lower down in the stream. It was also observed that the headwater inhabitants, as well as many naiads farther down the stream, were more compressed and of greater comparative length than the same species as it occurred in the larger part of the river.

The dam at Homer Park, 27 miles below Urbana, appears to form a barrier between the fauna above and below this obstruction. Above the dam, 19 species occur, while below the dam, 33 species have been observed. It is noteworthy that immediately above the dam the largest number of species found at one habitat was 14, while below the dam, at Homer Park, 28 species have been collected. It is probable that the fall of water over the dam aerates the stream and provides an especially favorable environment for the mussels.

## UNFAVORABLE INFLUENCES

Sewage pollution has killed all clean water life for a distance of fourteen miles below Urbana and has made the stream an unfavorable environment for a distance of twenty miles. Below this point the fauna is normal and is not affected by sewage conditions. In the desert area between St. Joseph and Urbana, slime worms and septic Protozoa were observed among the animals and foul water algae among the plants. A few beetles, breathing free air, were observed in the stream near St. Joseph and for some distance above this locality. Many of the old pond-like bodies of

water left on either side of the new drainage ditch are inhabited by clean water animals that occasionally get into the ditch during periods of high water. Fish, mollusks, and insects have been observed which doubtless came from this source.

#### PARASITES AND PATHOLOGIC AGENCIES

As a rule, parasites, either distomids or *Unionicola* (Atax) were rare in the naiads collected in the Big Vermilion and Sangamon rivers. Some of the *Anodontas* had marginal cists of distomids and many shells of this genus were discolored from this cause. Clark and Wilson (1912:61), in their study of the Maumee River fauna, observed distomids in various mussels which were believed to be the distomids described by Osborn and Kelly. The affected mussels were *Actinonaias ligamentina*, *Obovaria circulus*, *Elliptio gibbosus*, *Lampsilis ventricosa*, *Amblema undulata*, *Las-migona costata* (thought to be the distomid of Kelly), and *Anodonta grandis* (thought to be the distomid of Osborn). It is probable that these flat-worms also infest many of the mussels of the rivers investigated, but they were not observed in the specimens collected. *Cotylaspis insignis* and forms of *Unionicola* were also found by Clark and Wilson, but these parasites were not seen in the mussels examined from the area under consideration.

Pearls, usually of small size, were frequently seen attached to the shells of mussels, and many pearly growths cause by injuries were also observed. A large round pearl was found in a shell of *Anodonta grandis gigantea* from Crystal Lake, which measured almost a quarter of an inch in diameter (5 mm.). It has been suggested that many of these pearls and pearly growths attached to the mussels may have been caused by parasites, such as the distomids before mentioned. The same is also true of the round pearls found in the animal tissues of the mussels.

Crippled shells, those individuals have abnormal valves, were not common in either of the rivers examined. Mud was found to cause trouble in many cases, getting in between the mantle and the shell below the pallial line and causing large blisters.

#### ECONOMIC CONSIDERATIONS

The shells known as river mussels or Naiades are used in the manufacture of pearl buttons. As this industry, the making of pearl buttons, has reached large proportions it is imperative that the raw material be conserved for the maintenance of the industry. The continued fishing of the mussel beds in the larger rivers has greatly depleted the amount of available raw material—the mussel beds—, and the whole industry, shell collecting and button making, is threatened with disaster if means are not found to restock the depleted beds (see Coker, 1919:44). The United States Bureau

of Fisheries has conducted many interesting experiments on the propagation of mussels by the artificial infection of fish with mussel glochidia and the means and methods for restocking these cleaned-out areas are at hand. It only remains for proper laws to be passed and enforced, by the states or federal government, or both, regulating the time and place in which shelling operations may be carried on. Reasonable time must be given, at least three years, for the recovery of a depleted mussel bed.

In this connection it would seem that the mussel fauna of such a stream as the Big Vermilion River might form a reservoir from which the depleted beds farther down the stream might be restocked by fish which had been infected with glochidia from the commercial species living in the smaller stream. The Big Vermilion contains eleven species that are used for cutting button blanks and are considered valuable for this purpose by the button manufacturers. These are:

<i>Amblema undulata</i>	Blue point
<i>Lampsilis luteola</i>	Fat mucket
<i>Lampsilis anodontoides</i>	Yellow sand-shell
<i>Lampsilis ventricosa</i>	Pocket-book
<i>Tritogonia tuberculata</i>	Buckhorn
<i>Quadrula pustulosa</i>	Warty-back
<i>Quadrula lachrymosa</i>	Maple-leaf
<i>Actinonaias ligamentina</i>	Mucket
<i>Fusconaia rubiginosa</i>	Wabash pig-toe
<i>Lasmigona complanata</i>	White heel-splitter
<i>Lasmigona costata</i>	Fluted shell

Several of the smaller shells are also used when shells are scarce, as *Lampsilis compressa*, *Quadrula metanevra*, *Obovaria circulus*, and *Strophitus edentulus*. In the Sangamon River about the same number of species suitable for the button industry occur and these are usually of fine quality.

In their survey of the mussel fauna of the Kankakee basin, Wilson and Clark (1912:35) recognize the value of these smaller streams, with a fauna too small in individuals to be used by the shell fishermen, but containing many of the essential species from which good button blanks may be cut. These authors say: "The most valuable species are all good breeders throughout the basin. This, taken in connection with the excellent quality of the shells they produce and the good railroad facilities everywhere available, makes this basin one of the best yet examined for the supply of glochidia to be used in artificial mussel propagation." This statement might apply with almost equal force to the Big Vermilion, which may sometime be needed for a reservoir from which to propagate the mussels in the larger rivers.

Whether all of the fishes which have proved the most satisfactory hosts for glochidia are abundant here is not known, but as young of nearly all the

commercial shells were observed, it follows that the fishes carrying the glochidia must also be present.

The Big Vermilion River is seen, therefore, to be a valuable asset to the State, containing a fauna of both biologic and economic importance, which should be conserved for possible use as a restocking reservoir for the larger rivers. Pollution should be reduced to a minimum and the timber along the banks, especially of the headwaters, should be conserved in order that the water may be held in the ground and gradually flow into the streams, instead of running off in floods, causing excessive high water in the spring and extremely low water in the fall and winter. It would be possible to reforest many parts of the upper branches of the streams, where they are low or irregular places unfit for farming operations.



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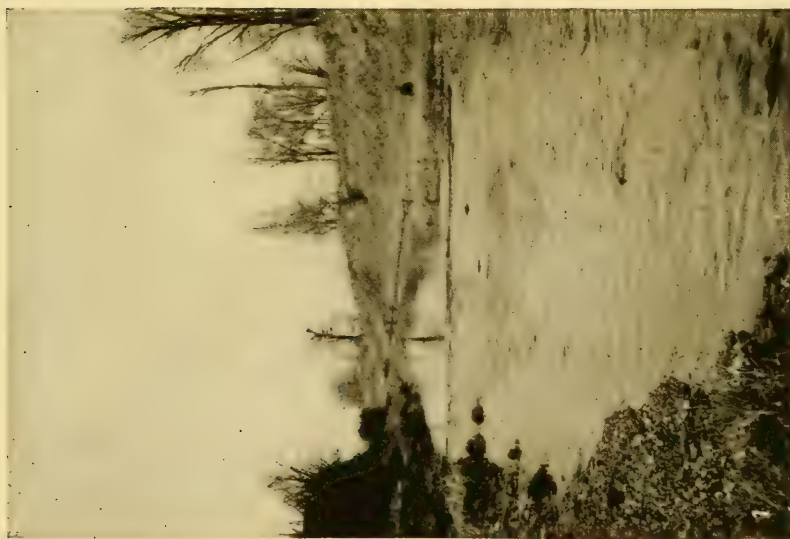
## PLATE I



## EXPLANATION OF PLATE

FIG. 1. Drainage ditch above Urbana, east of cemetery. Station 2.

FIG. 2. Salt Fork south of Muncie. Note water willow in center of stream bed; also numerous bare portions of stream bed, the river appearing as a series of pools. October, 1919. Station 26.





## PLATE II



## EXPLANATION OF PLATE

FIG. 3. Old stream bed of Salt Fork in Busey woods, north of Crystal Lake, Urbana. Original habitat for *Planorbis pseudotrivolvis*. Station 3.

FIG. 4. Junction of Middle Fork with Salt Fork to form the Big Vermilion River. Looking south from road bridge crossing Middle Fork. September 26, 1920.

FIG. 5. Middle Fork a fourth of a mile above junction with Salt Fork. Bed of river exposed in foreground. Station 29. September 26, 1920.





## PLATE III



## EXPLANATION OF PLATE

FIG. 6. Spoon River, seven-tenths of a mile above Salt Fork. Station 10. September 28, 1918.

FIG. 7. Spoon River, riffles below bridge, same locality as Fig. 6.





## PLATE IV



## EXPLANATION OF PLATE

FIG. 8. Bench mark 655, Salt Fork, above road bridge. Station 17. September 13, 1918.

FIG. 9. Salt Fork two and a half miles north of Sidney, looking north, the Champaign moraine on the left, a flood plain on the right. Station 18. September 13, 1918.





## PLATE V



## EXPLANATION OF PLATE

FIG. 10. Iron bridge one mile north of Sidney. Station 19. August 26, 1918.

FIG. 11. Cement bridge northeast of Sidney. Note large area of water lily, *Nymphaea advena*. Station 20, August 26, 1918.





## PLATE VI



## EXPLANATION OF PLATE

FIG. 12. Salt Fork three and a half miles above Homer Park, Station 23. October 4, 1918.

FIG. 13. Salt Fork. Deep pool below dam and rapids. Professor Smith's field laboratory during a period of twenty years. Station 25. November 4, 1920.





## PLATE VII



## EXPLANATION OF PLATE

FIG. 14. Dam in Salt Fork at Homer Park. The dam is just below the interurban bridge and is five feet high. November 4, 1920.

FIG. 15. Salt Fork below dam at Homer Park. Shallow water and rocky bottom. November 4, 1920. Part of Station 25.





## PLATE VIII



## EXPLANATION OF PLATE

FIG. 16. Salt Fork and mouth of Spoon River. Rowboat marks outlet of Spoon River through bar. September 24, 1920.

FIG. 17. Valley of Big Vermilion River from crest of bank at Gray's Siding. October 8, 1920.

FIG. 18. Cutting through shale rock covered with glacial deposits. Big Vermilion River one mile below mouth of Middle Fork. Station 30. October 8, 1920.





## PLATE IX



## EXPLANATION OF PLATE

FIG. 19. Rock bed of Big Vermilion River one mile below Middle Fork. Station 30. October 8, 1920.

FIG. 20. Sandbar in center of riverbed, several hundred feet below fig. 1. Station 30. October 8, 1920.

FIG. 21. Junction of Boneyard with Salt Fork. Boneyard on right above ice. December 20, 1919.



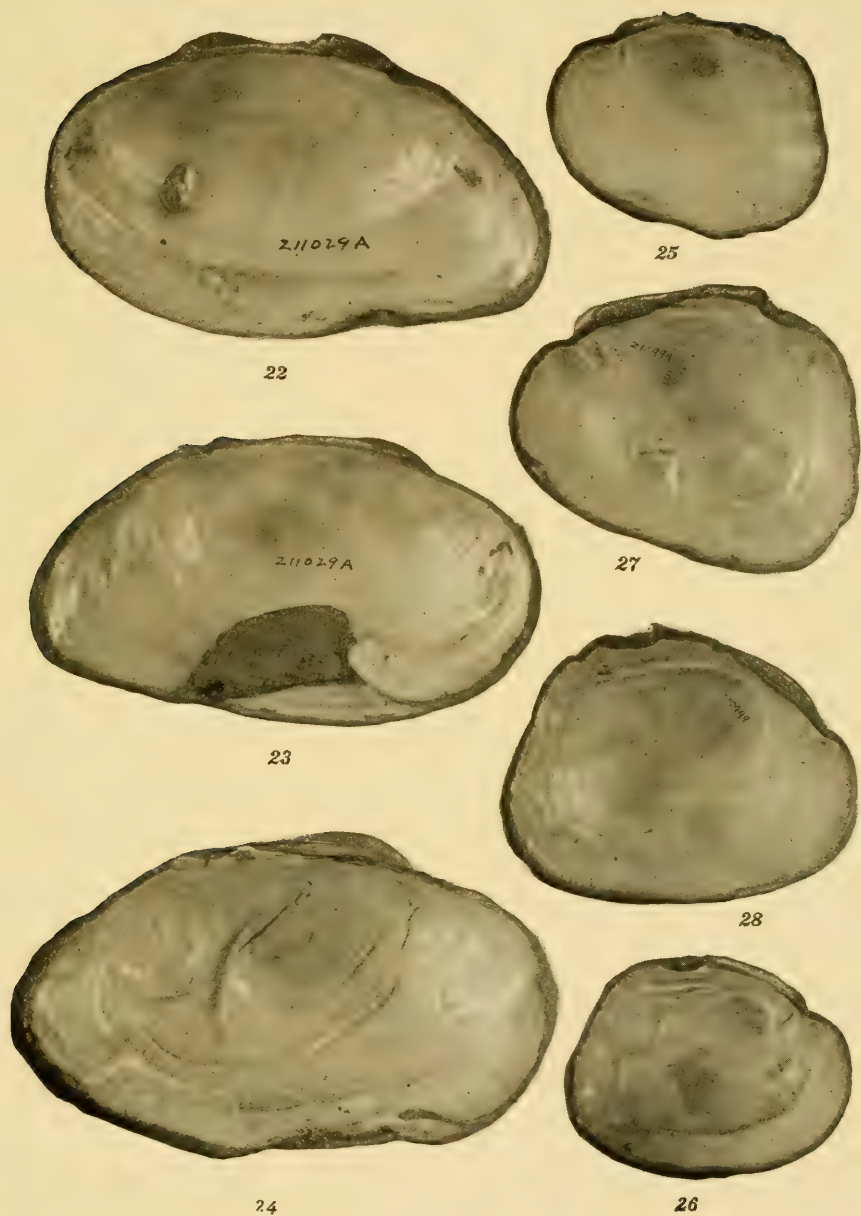


## PLATE X



## EXPLANATION OF PLATE

- FIG. 22. *Anodonta grandis*. Right valve with pearly growths at anterior end.  
FIG. 23. *Anodonta grandis*. Left valve with injured portion folded inward.  
FIG. 24. *Anodonta grandis*. Pearly formation in left valve.  
FIG. 25. *Amblyma undulata*. Right valve uninjured.  
FIG. 26. *Amblyma undulata*. Left valve with large blister inside pallial line.  
FIG. 27. *Amblyma undulata*. Left valve with abnormal pallial line.  
FIG. 28. *Amblyma undulata*. Left valve with pin-head pearls between pallial line and margin of shell.  
Pathologic mussels from Salt Fork.



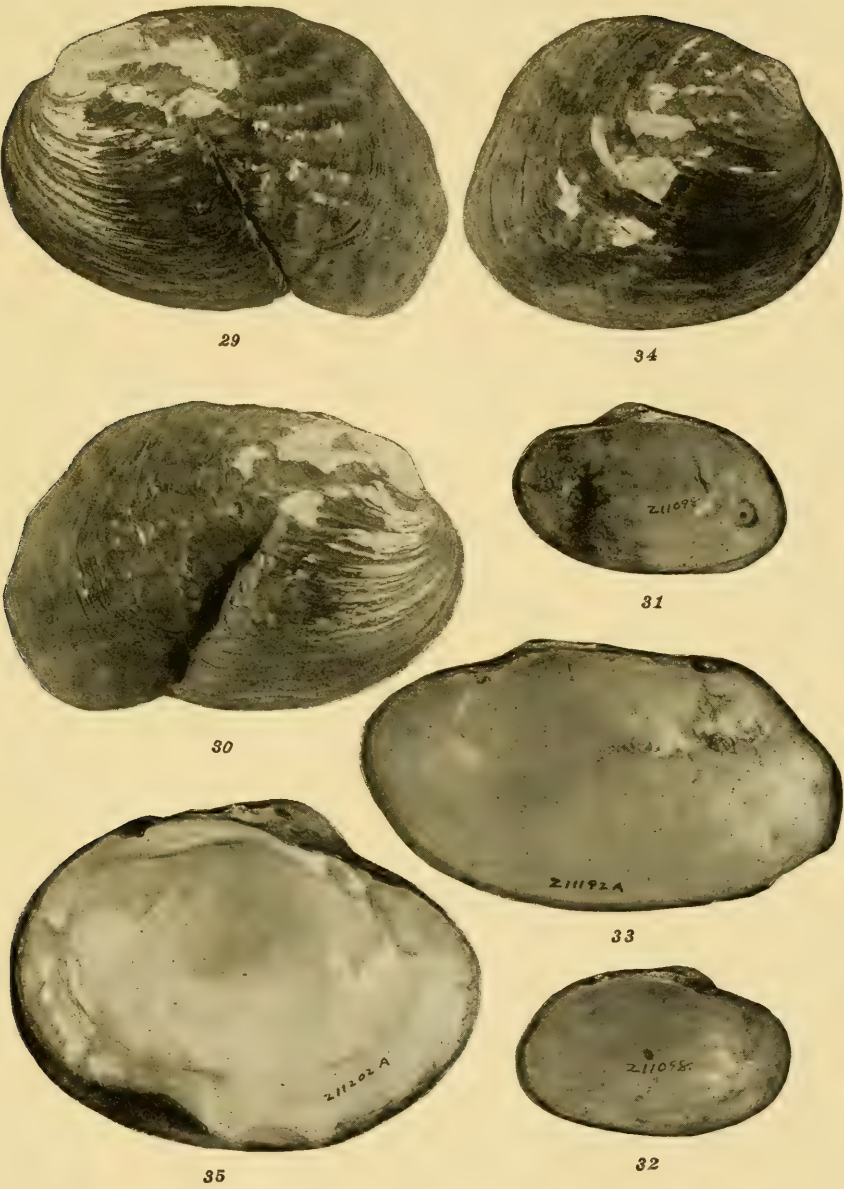


## PLATE XI



## EXPLANATION OF PLATE

- FIG. 29. *Amblema undulata*. Left valve with channel due to injury.  
FIG. 30. *Amblema undulata*. Right valve with ridge due to same injury.  
FIG. 31. *Strophitus edentulus*. Right valve with pearl near posterior end.  
FIG. 32. *Strophitus edentulus*. Left valve with distomid discoloration.  
FIG. 33. *Lasmigona costata*. Right valve with repaired injury near posterior end.  
FIG. 34. *Amblema undulata*. Spoon River form with rounded shell.  
FIG. 35. *Lampsilis ventricosa*. Left valve with injured postero-ventral margin.  
Pathologic mussels from Salt Fork.





## PLATE XII



## EXPLANATION OF PLATE

FIG. 36. Junction of Boneyard with Salt Fork canal, looking west. Note high bank on left where mussel shells were found, indicating bottom of bed of Salt Fork stream before the canal was dug. Sludge bank in foreground. September 14, 1920.

FIG. 37. Salt Fork canal three-fourths of a mile below first iron bridge east of Urbana. December 31, 1919.

FIG. 38. Farmer's bridge across Salt Fork canal, one-half mile below Brownfield Woods bridge. December 31, 1919.





## PLATE XIII

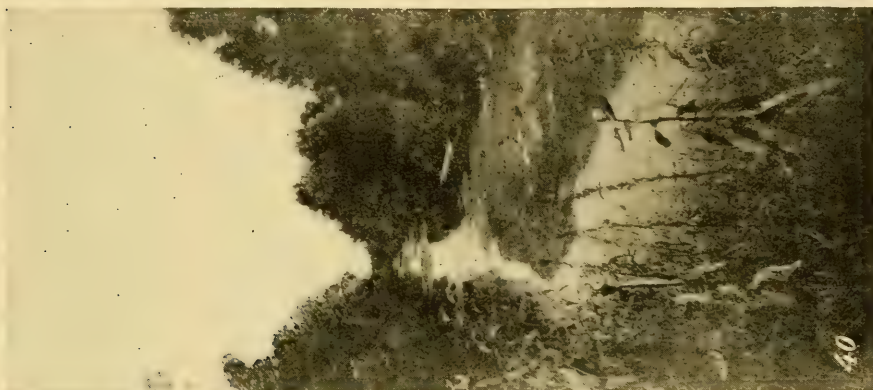
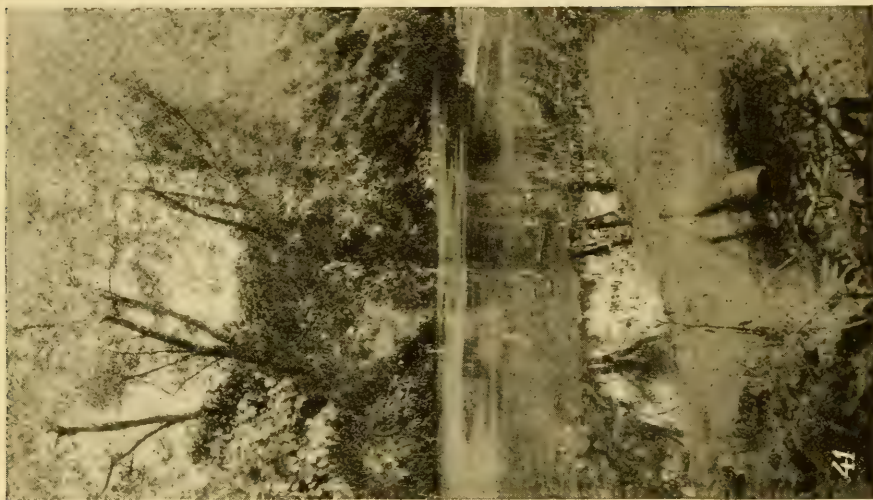


## EXPLANATION OF PLATE

FIG. 39. Boneyard just below Urbana septic tank outlet. September 14, 1920.

FIG. 40. Salt Fork canal west of Cottonwood's road bridge. Note bare sand bars with stream meandering between. Bars are covered with green putrescent matter dried by the sun. September 14, 1920.

FIG. 41. Salt Fork canal at entrance of small ditch from Champaign outfall pipe. Note sludge bank in foreground and sewage indicated by dark color of water in center of picture. September 14, 1920.





## PLATE XIV

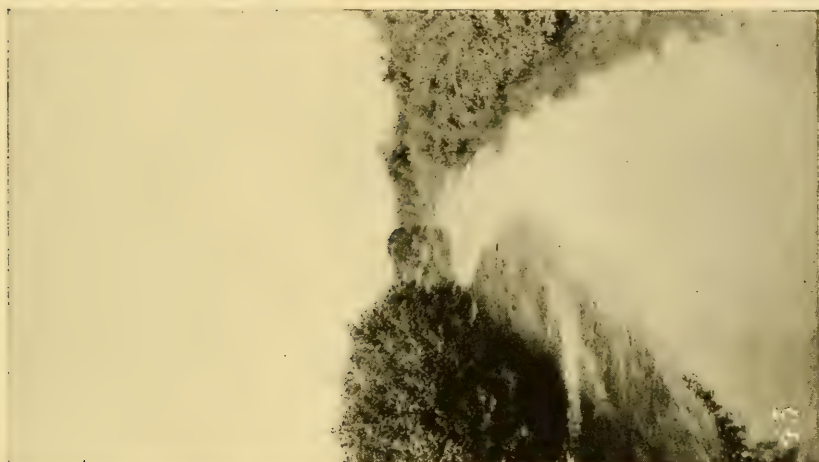
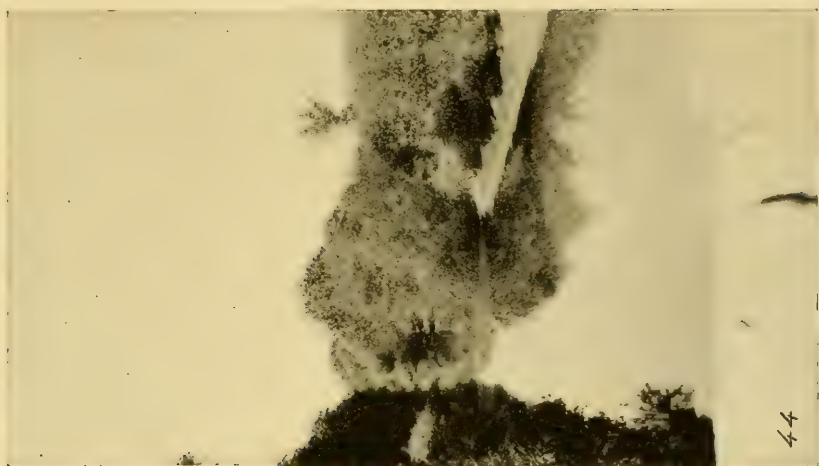


## EXPLANATION OF PLATE

FIG. 42. Salt Fork canal looking east from Cottonwood's road bridge. Note bare patches of bottom. September 14, 1920.

FIG. 43. Salt Fork canal looking southeast from last north and south road bridge. September 24, 1920.

FIG. 44. Salt Fork canal looking west from last farmer's bridge above St. Joseph. September 24, 1920.





## PLATE XV



## EXPLANATION OF PLATE

FIG. 45. Salt Fork canal looking south from last east and west road bridge west of St. Joseph. September 28, 1918.





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NORTH AMERICAN MONOSTOMES  
PRIMARILY FROM FRESH WATER HOSTS

WITH NINE PLATES AND TWO TABLES

BY  
E. C. HARRAH

Contributions from the  
Zoological Laboratory of the University of Illinois  
under the direction of Henry B. Ward No. 208

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE  
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1922

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## INTRODUCTION

The study of the Monostomata was undertaken four years ago following the suggestion of Professor Henry B. Ward, who expressed the need for a thorough study of the group. A preliminary survey of the available material served to convince me that a more complete and comparative study of the group was desirable and that such a study would prove of value to helminthologists. This study seemed more desirable since but two comparative studies of the group had been made in the last twenty-five years. The first of these was that of Stossich (1902) which is based wholly on European material; the second that of Kossack (1911) is based largely on the same material. The fact that very little had been done on this group in America and that no comparative study of the American fauna had been undertaken furnished further incentive for this work.

The writer undertook an investigation of the group which should be comprehensive in scope and at the same time comparative. For this purpose he had free and unlimited use of the large personal collections of Professor Ward secured thru extensive field work as well as obtained by exchange. These had been augmented, with a view to getting a complete series, by loans of material from European and American investigators. Unfortunately specimens of certain originals could not be secured either because they had been lost or because they could not be removed from the collections.

Thanks are due to the following investigators who at the request of Professor Ward kindly sent material from valuable collections for study and comparison; Professor Anton Collin, University of Berlin; Professor Theodor Pintner, University of Vienna; the curator of the Museum, University of Göttingen; Professor Fr. Zschokke, University of Basel; Dr. C. W. Stiles, Hygienic Laboratory, Washington, D. C.; Dr. B. H. Ransom, Bureau of Animal Industry. Dr. John C. Johnson has also very kindly loaned the writer material for study. For the study of *Cyclocoelum halli* and *Cyclocoelum wilsoni*, use has been made of the field notes of W. C. Hall filed with the records of that series.

Especially to Professor Henry B. Ward under whose supervision the work has been done, the writer desires to express most sincere thanks for the use of his extensive collections and of his library, as well as for his efforts to secure rare material and for the continued deep interest and hearty cooperation which have given the inspiration to finish this work.

## METHODS OF INVESTIGATION

The methods employed in this study are those ordinarily used with similar material. No special technique has been found necessary. In general sections were stained in toto with Erlich's acid hematoxylin and counterstained in section with alcoholic eosin. Sections were cut 10 to 20 micra in thickness. Frontal, sagittal, and transverse sections were used. In order to obtain a clearer perception of more minute and obscured parts wax reconstructions were made. These were employed particularly to find the relationship and constancy of form of the female genital organs.

## MATERIAL

The material on which this study is based is composed of various collections from different regions of the United States. It is limited to that obtained from North American fresh water hosts and in each instance is listed with the species description. However for comparison with the American material the following specimens were secured from the sources indicated.

## EUROPEAN MATERIAL

From the Zoological Museum, Berlin

<i>Species</i>	<i>Host</i>	<i>Cat. No.</i>	<i>Collector</i>
<i>Cyclocoelum problematicum</i>	<i>Totanus glottis</i>	2449	Ehrenberg
<i>Cyclocoelum problematicum</i>	<i>Totanus glottis</i>	2455	Ehrenberg
<i>Cyclocoelum problematicum</i>	<i>Canis vulpecula</i>	2454	Ehrenberg
<i>Cyclocoelum ovopunctatum</i>		1342	
<i>Cyclocoelum brazilianum</i>	<i>Scolapax flaviceps</i>	2494	v. Olfers
<i>Cyclocoelum tringae</i>		2495	Ehrenberg
<i>Haematotrepheus similis</i>	<i>Himantop. atropterus</i>	2486	Ehrenberg
<i>Haematotrepheus similis</i>		2309	Ehrenberg
<i>Monostomum vanelli</i>	<i>Vanellus cristatus</i>	1326	Rudolphi

From the Zoological Museum, University of Göttingen

<i>Cyclocoelum (Monostomum)</i>	<i>Gallinula chloropus</i>	284	Mehlis
<i>mutabile</i> (Zed.)	Taken at Claustal		
<i>Monostomum verrucosum</i>	<i>Anas bernicla</i>	234	Mehlis
<i>Monostomum attenuatum</i>	<i>Mergus merganser</i>	238	Mehlis
<i>Monostomum attenuatum</i>	<i>Anas fuligula</i>	220	Mehlis

From the Zoological Museum, University of Vienna

<i>Monostomum mutabile</i>	<i>Totanus flaviceps</i>	IX 552	
	Taken in Brazil		

From the Collection of Henry B. Ward, University of Illinois

<i>Collyriclum faba</i>	<i>Passer domesticus</i>	21.764	Zschokke
	Taken in Switzerland		

## NORTH AMERICAN MATERIAL

From the Leidy Collection

<i>Cyclocoelum leidy</i>	<i>Gallinago wilsoni</i>	160	Leidy
( <i>Monostomum mutabile</i> Zeder of Leidy)			

<i>Species</i>	<i>Host</i>	<i>Cat. No.</i>	<i>Collector</i>
<i>Cyclocoelum pseudomicrostomum</i> ( <i>Monostomum mutabile</i> Zeder of Leidy)	<i>Fulica americana</i>	186	Leidy
From the collection of the Army Medical Museum			
<i>Cyclocoelum obscurum</i>	<i>Stereolepsis</i> sp?	1035	Leidy
From the collection of the Bureau of Animal Industry			
<i>Notocotylus urbanensis</i> ( <i>Monostoma</i> sp. Stiles & Hassall)	<i>Dafila acuta</i>	5772	Stiles & Hassall
<i>Notocotylus urbanensis</i> ( <i>Monostoma</i> sp. Stiles & Hassall)	<i>Fiber zibethicus</i>	5769	
		5770	Stiles & Hassall
<i>Notocotylus urbanensis</i> ( <i>Monostoma</i> sp. Stiles & Hassall)	<i>Aix sponsa</i>	5771	Stiles & Hassall
<i>Notocotylus quinqueserialis</i> ( <i>Monostoma</i> sp. Stiles & Hassall)	<i>Arvicola riparius</i>	5773	Stiles & Hassall
From the Collection of Henry B. Ward, University of Illinois			
<i>Cyclocoelum pseudomicrostomum</i>	Wild duck	10.41	
<i>Cyclocoelum cuneatum</i>	<i>Gallinago delicata</i>	08.172	
<i>Cyclocoelum obscurum</i>	<i>Symphaemia semipalmata</i>	08.179	
<i>Cyclocoelum obscurum</i>	(unknown)	08.183	
<i>Cyclocoelum macrorchis</i>	Straight billed curlew	08.180	
<i>Notocotylus quinqueserialis</i>	<i>Fiber zibethicus</i>	15.120	
<i>Paramonostomum echinum</i>	<i>Fiber zibethicus</i>	21.91	
<i>Heronimus chelydrae</i>	Snapping turtle	08.176	
	<i>Emys blandingi</i>	12.161, 162, 163	
	<i>Chrysemys marginata</i>	N.B. 15, 21.760, 22.169	
	<i>Kinosternon odoratus</i>	16.425	
	<i>Cinosternum pennsylvanicum</i>	22.40, 41	
	<i>Graptemys geographicus</i>	22.166	
<i>Collyriclum colei</i>	<i>Passer domesticus</i>	11.11	L. J. Cole
		11.12, 21.961, 762	
<i>Cyclocoelum halli</i>	<i>Totanus melanoleucus</i>	21.90	W. C. Hall
	<i>Totanus solitarius</i>	21.763	W. C. Hall
<i>Cyclocoelum wilsoni</i>	<i>Gallinago delicata</i>	21.89	W. C. Hall
<i>Cyclocoelum triangularum</i>	<i>Tringa maculata</i>	21.88	W. C. Hall



## HISTORICAL DATA

More than a century ago the first of the Monostomata were described. Since that time many helminthologists have contributed to the study of this group. Most notable of the older authors are Zeder, Rudolphi, von Siebold, Van Beneden and Diesing. In more recent times Brandes, Stossich, Looss, Lühe, Monticelli, Kossack and Odhner have contributed materially to our knowledge of the European forms.

Apart from the work of Goeze (1782) who described two species which he believed to have only one sucker and that of Schrank (1788) which was a mere catalogue of species, Zeder (1800, 1803) was the first to establish this group. In 1800 he created the genus *Monostoma* based on five species; *Monostoma ocreatum*, and *Monostoma bombynae* which have since been removed to the distomes; *Monostoma verrucosum* a Notocotylid; and *Monostoma prismaticum* and *Monostoma mutabile* which are now transferred to the genus *Cyclocoelum*. Rudolphi in his *Synopsis Entozoorum* served in the early organization of the group. While a number of species were imperfectly known at this time it was not until the work of von Siebold (1835) was published that the anatomy of these worms was clearly understood. In this work the author gave a good description of *Monostoma mutabile* Zeder along with the early stages of the life history as shown in the development of the egg before it is discharged from the uterus. Diesing (1850) reorganized the genus including all species described up to this time. Following this Van Beneden (1861) reviewed the anatomy of *Monostomum mutabile* and added a description of the anatomy of *Monostomum verrucosum* Frölich with a study and description of a cercaria which he believed to be the larval form of this species. The next important contributions to the knowledge of this group were those of Monticelli (1892) in which he gave a complete account of the genus *Notocotyle* Diesing and in a second paper in the same year a similar account of *Monostomum cymbium* Diesing. Closely following these was the Revision of Brandes (1892) in which he proposed the new genus *Cyclocoelum* to include *Monostomum mutabile*, *M. flavum*, *M. arcuatum*, *M. tringae* and *M. ellipticum*.

In more recent time the work of Stossich (1902), Odhner (1905, 1907) and Kossack (1911) stands out as important contributions to the knowledge of this group. Looss and Lühe have likewise had a share in the organization of the group as a unit. The most recent European work on members of this group is that of Jegen (1917) in which he presents data on the life history and relationship of *Collyriclum faba* Bremser.

In North America little has been done on this group of trematodes and aside from the systematic arrangement of species by Pratt (1902) and the descriptive key of Ward (1918) only isolated descriptions of species have appeared. The earliest report of species which have been assigned to this group are those of Joseph Leidy (1856-1895) the descriptions of which are so meager that some of the forms must remain as species inquirendae.

MacCallum (1902) found and described *Heronimus chelydrae* from the lungs of the snapping turtle. Barker and Parsons fifteen years later re-described this form without reference to the work of MacCallum under the name *Aorchis extensus*. Barker and Laughlin (1911) described *Notocotyle quinqueserialis* from the intestine of *Fiber zibethicus* and later Barker (1916) described from the same host the new genus and species *Nudocotyle novicia*. These with the report by Cole of *Monostoma faba* (later named *Collyricum colei* by Ward) are the major items from North America. More recently Stunkard (1919) has shown that *Heronimus chelydrae* of MacCallum and *Aorchis extensus* of Barker and Parsons are identical, and Tyzzer (1918) from the study of *Collyricum colei* Ward and comparison of it with the description of *Collyricum faba* Bremser by Kossack, provisionally regards them as identical. Tyzzer's paper affords a detailed account of the anatomy of this species and a study of the maturation, fertilization and development of the miracidia within the eggs. His views regarding the identity of the two forms are discussed in detail later (p. 62-65).

#### SPECIES PREVIOUSLY DESCRIBED FROM NORTH AMERICA

Most descriptions of North American species of this group are inadequate and as a result of this it is impossible to determine with any degree of accuracy their rightful systematic position without re-examination of the material. This has been lost in a number of cases and in other instances all effort to locate certain specimens has proved futile. The following list is an attempt to bring together all references to date on the species previously described from North American fresh water hosts. Names indented represent later descriptions of the same form arranged in chronological order.

*Monostomum ornatum* Leidy 1856:43

*Monostomum ornatum* Brandes 1892:504-510

*Haematoloechus?* Stafford 1902:724

*Monostomum incommodum* Leidy 1856:43

*Distoma oricola* Leidy 1884:47

*Distoma oricola* Leidy 1891:414

*Monostomum affine* Leidy 1858:43

*Notocotyle? affine* (Leidy 1858) Barker 1916:183

- Monostomum spatulatum* Leidy 1858:111  
*Monostomum spathulatum* Leidy of Diesing 1859:426
- Monostomum asperum* Vaillant (nec. Nitzsch) 1863:6-7; 1863:347-348  
*Monostomulum asperum* Vaill. of Brandes 1892:504-511  
*Monostomum aspersum* Vaill. of Pratt 1902:966  
*Monostomum aspersum* Vaill. of Pratt, Ward 1918:382
- Monostomum mutabile* Zeder of Leidy 1885:9  
*Cyclocoelum leidy* nov. spec. of this paper
- Monostomum obscurum* Leidy 1887:24  
*Cyclocoelum obscurum* (Leidy) of this paper
- Monostomum amiuri* Stafford 1900:402
- Cyclocoelum vicarium* (Arnsdorff 1908) Kossack 1911:518  
*Monostomum vicarium* Arnsdorff 1908:362
- Notocotyle quinqu SERIALIS* Barker and Laughlin 1911:261-274
- Catatropis filamentis* Barker 1915: Pl. I, fig. 6  
*Catatropis fimbriata* Barker 1915:190
- Nudocotyle novicia* Barker 1916:175-184
- Heronimus chelydrae* MacCallum 1902:632-636  
*Aorchis extensus* Barker and Parsons 1914:193-194
- Collyrichum colei* Ward 1917:2-3  
*Monostoma faba* Cole 1911:42-48  
*Collyrichum faba* Tyzzer 1918:267-292

## NEW SPECIES DESCRIBED IN THIS PAPER

## Cyclocoelidae

## Cyclocoelinae

- Cyclocoelum leidy* nov. spec.  
*Cyclocoelum pseudomicrostomum* nov. spec.  
*Cyclocoelum macrorchis* nov. spec.  
*Cyclocoelum wilsoni* nov. spec.  
*Cyclocoelum halli* nov. spec.  
*Cyclocoelum triangularum* nov. spec.  
*Cyclocoelum cuneatum* nov. spec.

## Notocotylidae

## Notocotylinae

- Notocotylus urbanensis* (Cort)  
(Cercaria only known previously)  
*Paramonostomum echinum* nov. spec.

FAMILIES OF MONOSTOMIDAE

Altho in another section of this paper the monostomes are shown to be more closely related to other groups than to each other it is thought best to preserve the group classification until further evidence is secured which definitely proves the suggested relationship. For this reason the key to the monostome families is included and it is expected to serve only for the rapid determination of specimens rather than to furnish full diagnostic characters.

KEY TO FAMILIES

- 1(2) Intestinal crura anastomosing in the posterior end.....  
.....Family Cyclocoelidae
- 2(1) Intestinal crura ending blindly near the posterior end.....3
- 3(4) Testes lateral to crura.....Family Notocotylidae
- 4(3) Testes within crura.....5
- 5(6) Excretory pore posterior and terminal...Family Collyriclidae
- 6(5) Excretory pore dorsal; in anterior body half.Family Heronimidae



## DESCRIPTION OF FAMILIES

*Validity of the older name.*—The question raised by Lühe (1901) regarding the use by Looss (1899) of the family name Monostomidae Cobbold 1866 [erroneously credited to Monticelli by Lühe (1901) and by Stossich (1902)] without a type genus Monostomum and the extended discussion of Looss (1902) is a needless one if the rules of the International Code be applied. Article V of this code deals specifically with the family name which by the acceptance of the genus name Cyclocoelum becomes Cyclocoelidae.

## CYCLOCOELIDAE Kossack 1911

*Diagnosis.*—Endoparasitic trematodes of large to middle sized muscular bodies. Mouth opening terminal or subterminal surrounded by muscular sucker usually much reduced. Ventral acetabulum sometimes present, pharynx large, muscular; esophagus long. Intestinal crura simple or possessing internal ceca, anastomosing in the posterior end of the body. Excretory bladder between posterior intestinal arch and end of body with median dorso-terminal pore. Genital pore median, usually ventral to pharynx. Copulation organs present, well developed; seminal vesicle in cirrus pouch. Vitellaria in general lying between body wall and intestinal crura, sometimes surrounding the latter. Genital glands between intestinal crura, simple or lobed, forming the points of a triangle. Laurer's canal wanting; receptaculum seminis present. Uterus strongly developed lying in more or less regular folds between intestinal crura over which they sometimes extend, usually filling entire space between crura. Eggs numerous, without polar filament, usually containing well developed miracidia with characteristic double eye spots.

Parasitic in body cavity, lungs and nasal cavities of water birds.

Type and only American genus Cyclocoelum. Other genera Haematotrephus, Hyptiasmus, Typhlocoelum, Tracheophilus, Ophthalmophagus, Spaniometra and Bothriogaster.

The foregoing diagnosis differs from that of Kossack in noting that an oral sucker and a receptaculum seminis have been found in two genera of this family, namely Cyclocoelum and Haematotrephus. In the genus Cyclocoelum these organs have been found in the species described in this paper as well as in the following European species: *Cyclocoelum problematicum* Stoss., *Cyclocoelum ovopunctatum* Stoss., *Cyclocoelum brazilianum* Stoss., and in *Cyclocoelum tringae* (Brandes) as well as in *Haematotrephus similis* Stoss.

During the study of the Cyclocoelidae and the attempt to prepare a key the writer was impressed with the segregation of the genera into distinct groups. These groups are here designated as sub-families. The group composed of Cyclocoelum, Haematotrephus and Hyptiasmus are according to this grouping left in the sub-family Cyclocoelinae created by Stossich (1902) for the entire group. A second group is that formed by Typhlocoelum Stossich and Tracheophilus Skrjabin (1913) which on the basis of the strongly developed vitellaria and diverticula of the intestine deserve rank as a distinct sub-family to which I desire to assign the name Typhlocoelinae. As stated in a later section of this paper Cohn (1904) would ally this group with the Fasciolidae on the basis of a rudimentary sucker found in *Typhlocoelum flavum* (Mehlis). A third group is that formed by Ophthalmophagus and Spaniometra and is based on the position of the ovary in the intestinal arch with the testes anterior thereto, and on the position of the vitellaria which in these genera are ventral to the intestine. Bothriogaster is also placed in this group although it presents some striking differences, especially with respect to the vitellaria which in this genus are markedly like those of Cyclocoelum. However with respect to the reproductive glands it conforms more nearly to Spaniometra. Other peculiarities of this genus will be discussed elsewhere in this paper.

KEY TO SUB-FAMILIES AND GENERA

- 1(11) Ovary between testes or on a level with posterior testis.....2
- 2(8) Intestinal crura without diverticula.....  
.....Sub-family Cyclocoelinae Stossich 1902....3
- 3(6) Right and left sides of vitellaria separated at posterior end....4
- 4(5) Uterus loosely folded; long loops surrounding genital glands....  
.....Haematotrephus Stossich 1902
- 5(4) Uterus compact; loops short not surrounding genital glands....  
.....Cyclocoelum Stossich 1902
- 6(3) Right and left sides of vitellaria continuing into one another at  
posterior end.....7
- 7 Uterine loops extending laterally over intestinal crura and  
vitellaria to body wall.....Hyptiasmus Kossack 1911
- 8(2) Intestinal crura with distinct diverticula.....  
.....Sub-family Typhlocoelinae ....9
- 9(10) Testes strongly lobed.....Typhlocoelum Stossich 1902
- 10(9) Testes round.....Tracheophilus Skrjabin 1913
- 11(1) Ovary posterior to testes, situated in intestinal arch.....  
.....Sub-family Ophthalmophaginae ....12
- 12(15) Vitellaria ventral to crura.....13
- 13(14) Testes in posterior body half. Ophthalmophagus Stossich 1902
- 14(13) Testes in anterior body half.....Spaniometra Kossack 1911

- 15(12) Vitellaria lateral to crura.....  
       Ventral acetabulum conspicuously developed.....  
       .....Bothriogaster Fuhrman 1904

Up to the present the only genus in this family represented in North America is Cyclocoelum and for this reason the other genera are not dealt with in the following pages.

### CYCLOCOELUM

*Historical.*—The question of the type for this genus is indeed a complicated one and as Stiles (1908) has said “well represents a ship without a rudder.” Lühe accepts the designation of Hoyle (1888) and takes issue with Looss who by elimination accepts *Monostomum prismaticum* as type. Stiles (1908) presents a third view in which he says that the name *Monostomum* is a synonym to *Festucaria* by priority rule, since Zeder deliberately renamed the genus *Festucaria* Schrank (1788).

A critical study of the literature involved brings to light certain facts on this point which seem to the writer to be worthy of space here. The name *Festucaria* was proposed by Schrank (1788) for two species *Festucaria anatis* and *Festucaria strigis*. These species were described by Goeze (1782) in Klasse II of his family (genus) *Planaria* as “rundlichte oder walzenförmige Plattwurm” of which he says there are two genera. Only one of them is of concern here and is described by Goeze (1782:173–174) as having a single mouth, (“mit einfacher Mündung”).

From the context of the description one is led to believe that these worms were collected by Goeze since he says, “Ich, \* \* \* habe sie nur in zwei Arten von Vögeln gefunden; in einer zahmen Ente, und in einer grauen Weideneule.” He follows this with a description of the worms in situ as well as when he placed the intestine of the host in water where the worms “loosed themselves.”

The type of the genus *Festucaria* becomes by page precedence *Festucaria anatis* Schrank (1788). This purports to be the same worm described by Goeze (1782:174) as follows:—“In den Dedärmen einer Ente sassen hin und wieder kleine gelbliche Knötgen. Da ich einige abnehmen wollte, merkte ich, dass sie fest anklebten. Als ich sie ins Wasser brachte, gaben sie sich los, und ich erkannte sie für rundlichte Plattwürmer mit einer Mündung.” The description of his figure 9 plate 13 adds “(a) die einfache Mündung mit 2 Punkten; (b) eine Art von Maul darüber.” From the description and the figures this appears to be the crown of spines which Goeze mistook for a mouth.

The description of Schrank (1788), based on Goeze (1782), runs as follows:—

#### Splitterwurm—*Festucaria*

Ein länglichter, einförmiger Wurm vorne mit einer einzigen Saugemündung.



"Enten Sp. 54, Cylindri-formed, columnar, wälzenformig." "Zween erhabene Punkte in der Mundöffnung, *Festucaria anatis*." "Goeze Eingew. 174 tab. 13, figs. 8-11; in Enten."

Gmelin (1790) classifies the same worm as *Fasciola anatis*. Zeder (1800) renames the genus *Festucaria*, *Monostoma*, and includes under the name the following species;

*Monostoma elaphi*  
*Monostoma prismaticum*  
*Monostoma ocreatum*  
*Monostoma mutabile*  
*Monostoma verrucosum*  
*Monostoma bombynae*

In the same work the species of Schrank (*Festucaria anatis*) (*Fasciola* of Gmelin) is described as an Echinostome (*Distoma anatis*). Rudolphi (1801) recognized the same genus *Festucaria* Schrank with *Monostoma* Zeder as a synonym and later in the same paper (p. 62) stated that he permits the name *Festucaria* to stand even though Zeder had proposed a new one. This name he retained until 1809 when he rejects it for the denomination of Zeder which he says "omnino praeferenda sit." In his later paper (1819) Rudolphi still adhered to the genus name of Zeder. Subsequent to this time helminthologists have accepted without comment the genus *Monostoma* of Zeder. Consequently Hoyle (1888) designated *Monostoma mutabile* as type of this genus. Four years later Brandes (1892) in his Revision der Monostomiden grouped together what he believed to be members of this genus, "als gute Arten," *Monostoma mutabile* Zeder, *M. flavum* Mehlis, *M. arcuatum* Brandes, *M. tringae* Brandes and *M. ellipticum* Rudolphi and suggested their separation from the remaining species under the name *Cyclocoelum* with the following diagnosis: "Diese fünf Spezies scheinen ihrer Organisation und Lebensweise nach zusammenzugehören, jedenfalls die ersten 4, die sämtlich in der Leibes- oder Infrarorbitalhöhle von Wasservögeln schmarotzen, während *M. ellipticum* in der Lunge von *Rana maculata* gefunden wurde, \* \* \*. Die Enden der Darmschenkel mit einander verschmelzen, sodass der Darmtractus einem Ring darstellt." Looss (1899) accepted the revision of Brandes and named *M. mutabile* as type of the genus of Brandes. Later in the same notable work the author used the term *Monostomidae* to characterize a certain group of worms. But his contemporary Lühe (1900) in a review of the work of Looss objected on the ground of the nomenclature law to the use of the family name *Monostomidae* without a type genus *Monostoma* and called attention to the priority of the "völlig verschollenen" genus *Festucaria* Schrank. One year later Looss (1901) in explanation and confirmation of his earlier work showed by elimination that *Monostomum prismaticum* is type of the genus *Monostoma* Zeder. In regard to



the right of priority of *Festucaria* Schrank he stated that he found no reason to call back from oblivion that absolutely meaningless name. "Ich habe mich bisher nicht veranlasst gefühlt, diesen auch mir bekannten, aber in der That gänzlich der Vergessenheit anheimgefallenen und praktisch absolut bedeutungslosen Namen wieder ins Leben zurückzurufen; ich empfinde dafür auch heute noch keine Neigung und überlasse deshalb die Entscheidung der Frage mit Vergnügen denjenigen, die sich mehr dafür interessieren." Lühe continued the discussion on the basis of the priority of *Festucaria* Schrank and the deliberate renaming of Zeder. He stated, however, that he believes *Festucaria anatis* Schrank (based on Goeze 1782, Taf. 13, Figs. 8-11) to be *Echinostomum echinatum*. However Lühe continued to use the genus name *Monostoma* Zeder.

Stossich (1902) accepted *Monostoma mutabile* Zeder (1800) as the earliest record of the group and approved its removal by Brandes (1892) to the genus *Cyclocoelum*. He does not consider the priority of *Festucaria* or the renaming by Zeder (1800) but Zeder says distinctly that Schrank (1788) placed those worms with one sucker in a genus under the name *Festucaria* and that he (Zeder) in conformance to the German system of nomenclature wished to introduce the Greek term *Monostoma* which he considered a more appropriate and characteristic name.

Kossack (1911) cited the positions of Hoyle, Lühe, Looss and Stiles previously mentioned; he then avoids the real situation by accepting only the more generally recognized works and thus believes himself dealing with a necessity, and also to be in full accord with the law of priority. On this basis he omits from the discussion the genus name *Festucaria* and substitutes for the old name *Monostoma* the more significant name *Cyclocoelum*.

It seems to the writer that the case at hand is clearly covered by Article 32 of the International Rules of Zoological Nomenclature; and after a careful study of the case the writer is led to accept Stiles' view and to abide by the ruling of the International Commission according to which the genus *Monostoma* Zeder (1800) becomes a synonym of *Festucaria* Schrank (1788). The fact that Zeder did not include the original species, *Festucaria anatis*, in his genus does not affect the case since the genus name would remain with the type species; hence the redescribing of this form by Zeder under the name *Distoma anatis* does not change the case since in that event *Festucaria* falls with *Monostoma* into synonymy. Then *Festucaria strigis* having been removed to the genus *Strigea*, whether *Festucaria anatis*, is a distome (Zeder 1800), or an echinostome (Zeder 1803, Rudolphi 1809, and Lühe 1901), the case remains the same and can be analyzed only as a direct renaming of the original form. Accordingly the species of *Monostoma* Zeder fall in the genus *Festucaria* Schrank 1788. The type is clearly *Festucaria anatis*.

The opinion expressed by Lühe (1901) that he believes *Festucaria anatis* to be an echinostome, is indeed not a new view for in fact it is suggested in the description of Goeze when he describes the orifice as having above it a sort of a mouth. As was mentioned earlier in this work Goeze probably erroneously described the crown or ring of spines for the mouth. Also his description of the worms in situ in the intestine of a domestic duck suggests the probability of an echinostome. Zeder (1800) evidently recognized the distome nature of these worms for he described in his group Echinis under the name *Distoma anatis* worms which he terms identical with *Cucullanus conoideus* Bloch (1782), *Planaria enten* sp. Goeze (1782), *Festucaria anatis* Schrank (1788) and *Fasciola anatis* Gmelin (1790). Characteristic points of his description are the large acetabulum and the ring-like swelling around the head armed with spines. In 1803 this worm was described by the same author as *Distoma echinatum*. Rudolphi (1809) described *Cucullanus conoideus* Bloch, *Planaria (teres poro simplici)* Goeze, *Fasciola anatis* Gmelin, *Festucaria anatis* Schrank, *Distoma anatis* Zeder (1800) and *Distoma echinatum* Zeder (1803) as identical. Likewise Diesing (1850) and Baird (1853) interpret *Festucaria anatis* as identical with *Distoma echinatum*. This with the opinion of Lühe already given appears to be sufficient evidence to determine the probably Echinostome nature of *Festucaria anatis* Schrank. In any event the species described by Zeder (1800) as *Monostoma mutabile* which we now know as *Cyclocoelum mutabile* is quite strikingly different anatomically and hence clearly not closely related to *Festucaria anatis* based on the opinions of Zeder (1800, 1803), Rudolphi (1809, 1819), and Lühe (1901). From a study of the literature the writer is in agreement with the opinion of Lühe, Rudolphi and Zeder that *Festucaria anatis* is probably *Echinostomum echinatum* Rud. (1809). Whether these authors studied the same material can be only a matter of conjecture.

An additional fact, however, is furnished by our present knowledge of the normal habitat of these worms which with few exceptions are confined to partially closed cavities of the body, the infraorbital sinus, and areal sacs for *Cyclocoelum* and *Hyptiasmus*, and the trachea for *Typhlocoelum*. As has been previously noted the habitat of *Festucaria anatis* is the intestine of a domestic duck.

The genus *Cyclocoelum* Brandes (1892) was formulated to include the following species *Monostoma mutabile*, *M. flavum*, *M. arcuatum*, *M. tringae*, and *M. ellipticum* with the following description: first four species collected from the body cavity and infraorbital sinus of water birds the fifth *Monostoma ellipticum*, from the lungs of *Rana maculata*, with intestinal crura anastomosing in the posterior end.

In the acceptance of the genus name *Cyclocoelum* Brandes (1892) the writer realizes that he is subject to criticism on account of the genus

Cyclocoela Dujardin (1845) and in view of this fact calls attention to the recommendation of the International Zoological Commission in the International Code which reads:—"It is well to avoid the introduction of new generic names which differ from generic names already in use only in termination or in a slight variation in spelling which might lead to confusion. But once introduced, such names are not to be rejected on this account."

#### *Structure of the Genus*

The description of Stossich (1902) states that these worms are covered with spines which that author interprets of sufficient importance to be a specific characteristic. Although Zeder (1803) observed these granulations he was not able to determine their real nature and suggests that they are either cellular structures or glands underlying the thin cuticula. It was not until the work of Fuhrmann (1904) was published that the true nature of these, which are really pits became known. This author described and figured these pits as found on the ventral surface of *Bothriogaster variolaris* and stated that he has observed similar depressions on both the dorsum and venter of *Cyclocoelum mutabile*. However, he raises the question whether these are not a product of preservation. Kossack (1911) verified the work of Fuhrmann by similar observations on several species belonging to at least three distinct genera of this family. He supported the view of Fuhrmann as to their origin and added as evidence of their nonexistence in living material that the authors who had opportunity to study living material—notably von Siebold and Van Beneden—did not mention their presence.

There can be no doubt that Zeder (1800, probably also 1803) made observations on living material. That the particular observation mentioned above was made from living material of course is only a matter of conjecture. It is evident, however, that at least one author who studied living material did observe these pits. Hence the lack of mention by von Siebold and Van Beneden is not sufficient evidence to prove their nonexistence in living material.

That the state of contraction at the time of fixation is responsible for the degree of depth and apparent frequency of these pits remains unquestioned. But unless they occur in the living specimen it would be impossible to find them so regularly in preserved material. In addition if they are artifacts of preservation one would expect to find them in other trematides of similar size and structure.

While the writer has not had opportunity to study living Cyclocoelidae he has found the above mentioned "Grübchen" of Kossack, the "ovale depressionen" of Fuhrmann, constantly in more than one hundred and fifty specimens belonging to at least nine species of the genus *Cyclocoelum* and in *Haematotrephus similis*. While in the study of more than a hundred



specimens of *Heronimus chelydrae* MacCallum (1902) both living and preserved not a single instance has been found. For these reasons the writer feels safe in saying that these pits are characteristic of the living animal and are only emphasized by the state of contraction at the time of preservation. The various worms being fixed in different states of contraction would consequently show these pits more conspicuously in the more contracted specimens.

The body wall is composed of at least five layers. From outside inward they are as follows, cuticula, basement membrane, circular muscle, longitudinal muscle, and epithelium (Fig. 25). These compose what is commonly known as the dermomuscular sac. The disposition of the parts of the dermomuscular sac of this group agrees in most respects with the interpretation of Monticelli (1888) and Blochmann (1896). It differs however from the observation of Fuhrmann (1904) in which he says that the body musculature is differentiated into outer longitudinal, inner circular muscle layers and inside of this the layer of bands of diagonal muscles, in that the outer muscle layer is formed by circular muscles (Fig. 25). The single statement of Fuhrmann mentioned above is so strikingly different from all comprehensive works on this subject that the writer is lead to believe that it is a *lapsus calami* and that in reality the muscle layers of *Bothriogaster variolaris* are identical with those of other trematodes.

Zeder (1803) states that these worms have a single sucker on the forward end. His description of this organ is scanty and lacks the points which distinguish the sucker from the pharynx so that one is lead to believe in the light of present knowledge that he interpreted the pharynx in the Cyclocoelidae to be the same as the sucker in the Notocotylidae. Von Siebold (1835), the first to give a clear account of the anatomy of the Monostomidae in his description of *Cyclocoelum* (*Monostomum*) *mutabile* (Zeder), speaks of the mouth as a transverse oral opening leading to a funnel shaped canal which narrows gradually posteriorly and terminates in the so-called pharynx. No trace of a sucking organ was observed by this author.

Following this Van Beneden (1858) referred to the above work frequently but stated that the monostomes have only a mouth sucker situated in the anterior region. In another paragraph of the same work he speaks of the digestive system of Trematodes as showing generally an anterior sucker in the bottom of which is situated the mouth. This he says opens into a second enlargement similar to the preceding sucker, the pharyngeal bulb. In his figures of *Cyclocoelum* (*Monostomum*) *mutabile* (Zeder) the structure termed pharyngeal bulb above is indexed as buccal bulb. These show the pharyngeal bulb with no anterior sucking musculature surrounding the mouth opening. In a later paper (1861) the same author describing again this same species spoke of the bulb and the region preceding it which



he said is seen with difficulty. A little later in this work in the description of *Notocotyle* (*Monostomum*) *verrucosum* he employed the term "la ventuose antérieure ou plutôt le buccal," applying it to the spherical muscular bulb at the extreme anterior of this worm a Notocotyloid, evidently mistaking this structure for the same structure termed the pharyngeal bulb in the earlier work. His descriptions show clearly that the same organ which in the distomes is termed pharynx is here termed anterior sucker or buccal bulb.

Some years later Monticelli (1892) described the mouth as small in *Monostomum mutabile* and *Monostomum expansum*; of greater or less size in *Ogmogaster plicatum* and *Monostomum galeatum*; circular in *Monostomum hippocrepis* and *Monostomum trigonocephalum*; ellipsoidal in *Monostomum cymbium* and *Monostomum ornatum*. It is usually ventral and generally situated in the extreme anterior end. When present a prepharynx of variable length is situated directly in front of the pharyngeal sucker, the "anterior sucker or buccal bulb" of Van Beneden. Monticelli thus distinguishes between the funnel shaped tapering canal of von Siebold (1835) and the adjoining posterior structure; and designates it as a prepharynx. He says that in *Notocotyle* and some other genera of this family the prepharynx is wanting and that then the pharynx is anterior and plays the rôle of an anterior sucker. For this reason he designates this structure in these genera as a sucker pharynx.

Braun one year later, refers to the description of Monticelli and suggests that a sucking organ has been developed out of the pharynx. In 1901 the same author refers to the "bulbus buccalis" of Van Beneden, or pharynx of Monticelli, as a Mundsaugnapf which he says is followed by the esophagus. In another paragraph of the same work when describing *Monostomum trigonocephalum* Rud. (since removed to the genus *Pronocephalus* by Looss) collected from the intestine of the sea turtle he says that the sucker is 0.12 mm long and 0.09 mm broad and again states that it is followed by a straight esophagus 0.3 mm long, without a pharynx. Thus Braun has construed the muscular structure at the extreme anterior in the Notocotyliidae, Pronocephalidae and other families of this group to be a development of a structure similar to that termed pharynx by Monticelli in the Cyclocoelidae.

Barker and Laughlin (1911) accept this view without comment and describe the worms *Notocotyle quinqueserialis* as clinging to the intestine of the muskrat tenaciously with the well developed oral sucker. They found no evidence of a pharynx.

Taschenberg (1879) describes the mouth in the genus *Didymozoon* as an opening followed by a funnel shaped duct leading to the pharynx. This he states to be generally characteristic of the entire group. Lönnberg (1891) found in *Didymozoon lampridis* the well developed sucker (pharynx of

Taschenberg) and just posterior to it a very small muscular bulb the pharynx. Odhner (1907) finds in *Didymozoon scombri* Tschbg. a similar pharyngeal bulb which he figures and proves beyond doubt that the pharynx of Taschenberg is a very strongly developed sucker followed by an extremely small pharynx. In this same notable work he says that in *Cyclocoelum* (*Monostomum*) *mutabile* (Zeder) and other parasites where only a pharynx is present that there is always a region anterior to it which he terms the "Mundrohr" or "Mundhöhle" (prepharynx of Monticelli), a structure which by the contraction of the inner walls changes the pharynx into a sucker. This same region is shown in the figures of Odhner for *Didymozoon scombri* Tschbg.

Looss (1899) speaks of the mouth sucker but gives no equivalent for the pharynx of Monticelli. Later, however, he interprets the swelling at the beginning of the esophagus in *Microscapha reticularis* as a pharynx. Cohn (1904) calls this to account when he states that this swelling is nothing more than the esophageal sphincter which is present in many species. The same author interprets the oral sucker of Looss, or buccal bulb (anterior sucker) of Van Beneden, as a pharynx and adds that it is his opinion that soon monostomes will be found with a well formed sucker adjoining a typical pharynx. The evidence given in support of this consists of the statement that *Haplorchis cahirinus* Looss has a strongly developed pharynx preceded by a rudimentary sucker and that he has observed in *Cyclocoelum* (*Monostomum*) *mutabile* (Zeder) and in one other species (to be published later) a rudimentary sucker. On the contrary Looss (1899) figures *Haplorchis cahirinus* with a well developed but small oral sucker followed by a somewhat smaller but perfectly developed pharynx and in his description of this species states specifically that the oral sucker and the pharynx are well developed structures. He regards the rudimentary structure occurring on the ventral side as an acetabulum. He adds also that the nerve commissure which according to Braun lies in all the Digenea more or less bent around the dorsal side of the oral acetabulum and the pharynx, is in front of the muscular sucking organ in the Monostomidae and therefore that organ is a true pharynx, tho this organ serves both as a sucker and a pharynx.

Stossich (1902) calls the pharynx of Monticelli an "inner sucker" which he says serves the same function as the mouth sucker of other trematodes.

Odhner (1907) states that those that acquire holdfast organs in the least degree are the parasites of the respiratory organs; the group containing *Cyclocoelum mutabile* being entirely suckerless. Kossack following the decision of Monticelli says that the question can be determined only by a study of the position and distribution of the nerve ganglia. Consequently he termed the anterior muscular structure a true pharynx. Ward (1918) calls the same structure the oral sucker and says that no pharynx is

present. The interpretation of Braun, Looss, Ward and others is indeed well exemplified in many cases where the anterior region is telescoped posteriad over the opened anterior portion of the pharynx (Fig. 46).

Records of an oral sucker in this group are few, aside from that found in *Cyclocoelum mutabile* by Cohn (1902). Wedl (1857) gives an account of the oral sucker in *Monostomum lanceolatum* as follows:—"Der kleine Mundnapf liegt an der Bauchseite des zugeschmälerten Vordertheiles des Thieres (Fig. 15a) und ist nach rückwärts von einem dickfleischigen *Bulbus oesophagus* (b) begrenzt, \* \* \*". These with the account of the writer (Harrah 1921) in which the oral sucker was described in two species of this genus constitute the evidence produced to demonstrate the presence of the oral sucker in this group.

In the light of the foregoing the question brought out by a long continued controversy remains unsettled. Is the structure termed the pharynx by Monticelli (1892) phylogenetically a pharynx or an oral sucker? While Monticelli attempted to prove by the distribution of the anterior nerves that the muscular bulb, or pharynx as he termed it, was a true pharynx, this has not been generally accepted and hence remains a matter of much controversy. In the opinion of the writer the brain commissure which lies distinctly anterior to the pharynx (Fig. 8) can be used as a land mark only and in a different state of contraction might have its relative position changed. The innervation is no doubt distributed to the other anterior structures as well. Although the nerve commissure has the same relative position in the distomes this alone does not prove the phylogenetic origin of the pharynx, and when a muscular sucking apparatus is found and proof established of such an organ anterior to and adjoining the pharynx, as predicted by Cohn (1904), then and only then can these organs be safely designated as oral sucker and pharynx.

In this study the writer has examined more than one hundred specimens of the genus *Cyclocoelum* Brandes comprising at least fifteen different species. In this material different conditions are found. In *Cyclocoelum obliquum* Harrah 1921, *Cyclocoelum halli* nov. spec. *Cyclocoelum obscurum* (Leidy), *Cyclocoelum triangularum* nov. spec. a very weak and scarcely distinct oral sucker is present. The concentration of tissue is scarcely discernible except under the best optical conditions and even in sections there appears only a concentration of tissue at this point (Figs. 36-42). The outer circular band or sheath is found to be very light and not a continuous band as in *Cyclocoelum elongatum*. The above condition has been found to obtain in *Cyclocoelum problematicum* Stoss. and *Cyclocoelum tringae* (Brandes). In these species the sucker musculature is easily overlooked and when not taken into account the mouth opening agrees well with the structure so clearly described by von Siebold (1835) and van Beneden (1858) and that named prepharynx by Monticelli (1892). On the



other hand in *Cyclocoelum pseudomicrostomum* an intermediate condition is found. On first observation the mouth opening appears like the one just described; however, on more careful scrutiny a light but well formed sucker is discernible. In this case, however, the longitudinal and oblique muscles are actually increased immediately surrounding the buccal duct which leads inward toward the very muscular pharynx (Fig. 43). From this more or less muscular wall, radial muscles extend outward having their origin in a weak band of circular muscles. This outside covering of the sucker is held in place by the same sort of transverse muscles as in the distomes. Were this the only case found one could perhaps accept Cohn (1902:715) who has observed what he terms a rudimentary mouth sucker in *Cyclocoelum mutabile* (Zeder).

The maximum condition observed by the writer was that found in *Cyclocoelum elongatum*, in which posterior to the opening of the mouth, which is downward as before, is seen a large weak oral sucker scarcely visible in toto preparations. It is from one-third to one-half larger than the pharynx posterior to it and extends from the extreme anterior of the animal to well over the anterior portion of the pharynx. It measures  $314\mu$  in length by  $463\mu$  in width. The musculature is much less strongly developed than that of the pharynx and consists of an outer circular layer connected by radial, longitudinal, and oblique muscles to a much heavier inner circular band which forms the muscular walls of the mouth (Figs. 44, 45, 47, 48). This muscular body is suspended by much lighter strands of transverse muscle having their origin in the musculature of the body wall and their insertion at times in the outer circular band of muscles covering the sucking musculature and again in the radial muscles of the sucker itself. In general the position of this sucker is such that it opens downward but suspended as it is a slight contraction of the dorsal suspensory muscles and at the same time a relaxation of the ventral ones could easily give to the sucker a different position so that its aspect would be changed from that of its true antero-ventral one (Fig. 29).

In all specimens studied the writer has found evidence of the oral sucking mechanism and believes it to be a universal character in this family. In a study of *Haematotrephus similis* Stossich a sucker almost as heavy as that of *Cyclocoelum elongatum* was found (Fig. 28), and in the former species the sucker is considerably more prominent than in *Cyclocoelum pseudomicrostomum* and *Cyclocoelum mutabile*. *Cyclocoelum microstomum* could not be obtained for study of this feature.

Following the oral sucker is a thin walled, lightly muscular tube extending posteriad and ventrad to the pharynx and opening into it on the ventral side. The writer believes this to be a condition due to the state of contraction at the time of preservation and that in a fully extended specimen the oral opening would enter the pharynx from the anterior face,



thus leaving some 150 to 200 $\mu$  between the oral sucker and the pharynx. This portion is termed the prepharynx (Fig. 29).

As will be seen by the description which is to follow later the structure of the pharynx is practically identical in many of the species of this and other families and therefore must necessarily have developed from a similar tissue in a similar manner. This being the case there remains the functional differentiation which may come about in the absence of a well developed oral sucking structure. No doubt the pharynx aids the weak sucker in drawing in food and it is highly probable that the suction produced by these heavy muscular walls is indeed very great. As was stated earlier in this discussion the position of the oral sucking apparatus relative to the pharynx in all those species which do not possess a strong oral sucking apparatus strongly indicates this view.

As was stated before the muscular bulb, or pharynx of Monticelli, is identical in structure and has no doubt arisen in the same manner in all the species of this family. Even though it may function as a sucking organ in some instances this structure has not been modified and does not appear to be typical sucker tissue as it has been described in other trematodes. If, however, this muscular organ is present in one or more species of this genus at the same time with a distinct anterior musculature which is typical of that tissue as found in other groups of trematodes and is constant in these species, then one is justified in designating the anterior musculature a sucking organ or oral sucker and the musculature posterior to it a pharynx as it was termed by Monticelli (1892).

Immediately posterior and dorsal to the prepharynx is a muscular structure developed around the wall of the posterior prepharynx or anterior esophagus. On first observation the pharynx appears as two bean-shaped halves lying one on either side of the anterior portion of the esophagus. On more careful study, however, it is found to consist of heavy muscular halves bound together on the edges by smaller bands of fibers so that in the true cross section it appears as a cylinder with an elongated dorso-ventral slit passing through it.

The pharynx is variable in size and form within the species as well as in different species, and may be in some species distinctly elongated while in others it is noticeably expanded laterally and still in others it is spherical. It measures in *Cyclocoelum pseudomicrostomum* 778 $\mu$  and is slightly longer than broad. In *Cyclocoelum obscurum* it is in general spherical and measures 215 to 298 $\mu$ . In *Cyclocoelum macrorchis* it is distinctly longer than broad and measures 264 to 314 $\mu$  in length by 198 to 248 $\mu$  in width. In *Cyclocoelum elongatum* the pharynx is oblong measuring 264 to 331 $\mu$  in length by 215 to 281 $\mu$  in width. While the range of measurements gives a general idea of the size and shape of the pharynx this study has shown

that the individual which has the longest pharynx is not always the one which has the narrowest one and vice versa.

As stated above the size and form of the pharynx is not constant as might be indicated by an average or range of measurements. *Cyclocoelum obscurum* shows eight instances in which the pharynx is round, two with a greater width than length, one with a greater length than width; this gives an average for eleven specimens of  $230\mu$  in length and  $231\mu$  in width, agreeing closely with the record that eight of the eleven cases cited show the pharynx to be spherical. From the range one would infer from the maximums that the pharynx is spherical but from the minimums of less transverse diameter than longitudinal. In *Cyclocoelum macrorchis* and *Cyclocoelum elongatum* every specimen measured shows for the pharynx a greater length than width while in *Cyclocoelum pseudomicrostomum* and *Cyclocoelum obscurum* some were spherical while the majority have a greater length than width. From this comparison one can see readily that the pharynx possesses such variability in size and form in this genus that it can be termed at best only spheroidal.

The musculature of the pharynx is, as stated previously, similar in all the species of this genus and consists of numerous fibers bound into bundles that are so interlaced as to make a very powerful organ and in the absence of the strong oral sucker it is quite probable that it serves as a sucking organ as was stated earlier in this work.

The musculature is quite characteristic of this organ as it has been described in other trematodes and consists of circular, radial and longitudinal fibers. The circular muscles are most numerous and constitute approximately 75 percent of the entire structure. They are pierced by bundles of radial muscles which have their origin in the outer layer of circular muscles and their insertion in the inner layer of the same muscles whose fibers intertwine all the muscles of the circular and radial type, particularly at their origin and insertion.

In most cases this muscular bulb stands with the anterior end open thus forming a continuation of the funnel shaped mouth opening to the posterior end of the pharynx which in all instances observed by the writer is closed just anterior to the esophagus that leads caudad from this organ.

The esophagus is a thin walled tube of varied length. In *Cyclocoelum elongatum* it measures 347 to  $463\mu$ ; in *Cyclocoelum obscurum* 331 to  $662\mu$ ; in *Cyclocoelum halli*  $483\mu$  on the average. The wide range of variation in length is due to the fact that the esophagus takes an S-shape (Fig. 29) which is no doubt due to a state of partial contraction taken at fixation. This condition makes it impossible to secure the exact length of this organ. Because of the different states of contraction the esophagus is more sinuous in some specimens than in others and consequently shows a much greater variation in length. In view of this fact the writer can place very little

weight on the exact length of the esophagus as a specific characteristic. In fact in some cases where the toto specimen showed the esophagus to be very short, sections of the same specimen gave evidence of a relatively long but much folded tube due no doubt to contraction.

In the case of *Cyclocoelum obscurum* stated above the length varies from 298 to 662 $\mu$  making an average for the eleven specimens of 419 $\mu$ . Under the conditions mentioned the average does not represent the actual length of the esophagus. It was noted from a study of this collection that the esophagus of one individual was more than twice as long as that of another. However, the maximum length of the esophagus is not represented by the maximum measurements secured since in no case has the writer observed the esophagus when it could be said to form a straight line from the oral sucker to the pharynx. The normal condition is represented in figure 29 where the esophagus arises at the dorsal portion of the pharynx and from there takes a winding course both laterally and dorso-ventrally to the intestinal bifurcation into which it empties directly from the ventral side of the latter organ. The esophagus bifurcates at the posterior portion of the first body sixth to form the intestinal crura. One branch passing to the right, the other to the left side of the body, thus forming an arch which lies in the anterior one-sixth of the body. The crura extend from this parallel to the body wall, being separated from it only by the vitellaria, to the extreme posterior end where they anastomose forming a posterior arch. This is separated from the posterior body wall by the excretory bladder. The crura are usually large with a large lumen. However, in some cases they are extremely irregular and show in a few instances more or less distinct pouches which in some individuals appear as distinct diverticula and in fact are as strongly exemplified as some of those shown by Stossich (1902) and Kossack (1911) for the genus *Typhlocoelum*. This feature, however, is not constant for any species of the genus *Cyclocoelum* observed by the writer and is probably due to the pressure produced by expanded uterine loops which fill out the space between the crura and in many instances reach over the crura. Anterior to the intestinal bifurcation in *Cyclocoelum macrorchis* and *Cyclocoelum obscurum* there is an evagination which makes a pronounced undivided neck to the crura into which the esophagus opens. This appears in every specimen of the fifty-six in the two collections. This condition is in decided contrast to the other species studied. In these specimens, however, the intestinal crura are comparatively empty and show a generally relaxed condition whereas in most of the other specimens the crura are well filled and apparently well extended. It is probable in view of the relaxed and empty condition of the crura of the former species that the neck of the bifurcation is the result of the condition rather than a constant character for the species.



The excretory system of these worms cannot be fully made out in preserved material and at most one can obtain accurate knowledge of only a small part of this system without having had opportunity to study developmental forms while living. In general the excretory bladder can be made out in all species as a simple flattened sac, except in *Cyclocoelum elongatum*, lying between the posterior arch of the intestine and the body wall, usually closely approached on either side by the posterior extremities of the vitellaria. It opens to the exterior on the median dorsal surface by a small duct surrounded at its exterior opening by a strong sphincter. Two main branches of the system open into the excretory bladder one on either side. These branches follow in general the course of the intestinal crura and are joined by many secondary branches which anastomose freely forming a vast net-work ramifying the entire body. The ducts of the system are composed of relatively heavy muscular walls which aid in the movement of the excretory products toward the bladder.

The nervous system so far as has been made out from the material at hand does not differ materially from the description of Lang (1880). The cephalic ganglia are situated one on either side of the pharynx and are connected by a dorsal commissure which spans the anterior alimentary organs between the pharynx and the sucker. In the miracidia are seen the beehive-shaped eye-spots first observed by Van Beneden (1861) and later described by Faust (1918).

The vitelline glands in this family are very much alike in all genera being composed of two main canals which lie parallel to and usually outside of the intestinal crura. From these main stems side branches go out both dorsally and ventrally. The glands are made up of small follicular bodies arranged around the ducts so as to form grape-like clusters. The development of these glands is constant within a species and may be built up on the main stem with relatively few branches. The strongest development of the secondary branches is found in *Cyclocoelum microstomum* and *Cyclocoelum pseudomicrostomum* and in the genus *Hyptiasmus* where the branches of the vitelline glands form a net-work closely applied to the intestinal crura. The vitelline substance is conveyed to the ootype by a duct from each side in the region of the ovarian complex; these pass to a point posterior to the shell gland where they unite. At the point of union is usually found an enlargement, the vitelline reservoir. The duct then passes to the dorsal side of the shell gland where it becomes embedded in the latter organ; however, it emerges from this to re-enter it on the anterior dorsal surface and just after its entry joins the oviduct at the point of its enlargement to form the ootype.

The cirrus pouch as stated by Kossack (1911) shows little variation. It is a clubshaped muscular pouch containing a relatively large vesicula seminalis to which unites a short weakly developed pars prostatica. This



gives rise to a relatively large cylindrical unarmed ductus ejaculatorius. In most individuals the ductus ejaculatorius and pars prostatica are much coiled inside the cirrus sac and can be made out only with considerable difficulty. The writer has had the good fortune to have for study two specimens of *Cyclocoelum brazilianum* Stoss. one of which has the ductus ejaculatorius protruded from the body. The other one with the ductus ejaculatorius extended into the uterus in a case of evident self-copulation. (Figs. 31, 35). In these specimens the ductus is in excellent position for study and appears as described above. Through the union of the end portion of the cirrus pouch and the uterus a relatively large genital atrium is formed.

The form of the genital glands throughout the family is in general very similar. They are usually round or elliptical, sometimes flattened from pressure of the surrounding parts, with the exception of *Cyclocoelum vicarium* (Arned.) and in the genus *Typhlocoelum* in which species the testes are lobed. The genital glands of the genus *Cyclocoelum*, the only American genus thus far known belonging to this family, are spherical in form. The testes are located so the posterior is in or near the posterior intestinal arch and the anterior, a greater or less distance from this, separated often by uterus loops. Exceptions to this are found, however, in *Cyclocoelum oculobium* (Cohn) and *Bothriogaster variolaris* Fuhrmann in which the ovary occupies the posterior intestinal arch while the testes are situated in the middle region of the body. The vasa efferentia given off from the testes unite a short distance anterior and median to the anterior testis in *Cyclocoelum obscurum*, to form the vas deferens which makes its way between the uterine loops to the cirrus pouch previously described. The ovary is spherical and communicates by a short duct to the compact closely lying shell gland.

The presence of the receptaculum seminis and Laurer's canal have been held in question since the earliest accurate work on the anatomy of these worms, that of von Siebold (1835) who described in *Monostomum mutabile* as organs contributing to the formation of the egg four distinct glands, the vitellaria, which he interpreted as the ovary as follows:—"Die Ovarien bilden kurze blinde Schläuche, die unter einander anastomosiren und den Darmkanal, nachdem er vom Oesophagus aus die Seitenränder des Leibes erreicht hat, in seinem ganzen weiteren Verlaufe wie ein Netz umgeben. Es ist dies eine eigenthümliche Anordnung, die ich bis jetzt noch bei keinem anderen, zu den Trematoden gehörigen Wurme angetroffen habe." The three other parts having to do with the formation of the shell are described by the following characteristic statements:—"An der zweiten Abtheilung der weiblichen Geschlechtstheile, die zur Bildung der Eierschale bestimmt zu sein scheint, lassen sich deutlich drei eigenthümliche Organe erkennen. a) Erstens fällt hier ein runder, weissgelber Körper

in's Auge, der zur rechten Seite dicht neben und vor dem hinteren Hoden liegt, und an Umfang etwas kleiner als dieser ist. b) Diesem runden Körper hängt zweitens nach innen ein ovaler, noch kleinerer und ebenfalls weissgelb gefärbter Körper an, der mit ersterem durch einen kurzen, anfangs weiteren, nachher engeren Kanal in Verbindung steht. c) Endlich liegt drittens, theils unter diesen Organen, theils zwischen dem runden Körper und dem hinteren Hoden eine durchsichtige, fast farbelose und unregelmässig umgränzte, feinzellige Masse, in die der gemeinschaftliche kurze Ovariengang einmündet, und aus der der eierführende Uterus hervortritt. Es ist mir bis jetzt nicht gelungen, eine Verbindung dieses unregelmässigen Organes mit dem grösseren runden Körper bestimmt nachzuweisen; doch bin ich überzeugt, dass eine solche wirklich existirt." Van Beneden (1861) in his study of *Monostomum mutabile* after characterizing the vitellaria (vitellogène Van Beneden, Ovarien von Siebold) and the ovary (germigène Van Beneden, one of the shell forming organs of von Siebold) says (p. 74), that besides the testes and the ovary only one other organ has been observed by him in the posterior region i.e., the vitelline duct which dilates to form the vitelline reservoir. In regard to the other organs described by von Siebold (1835) he says "Sont-ce là les deux autres organes que M. von Siebold signale et qui contribuent à la formation des oeufs? Cela est probable!"

More recently Braun (1892) stated that he is able to find the receptaculum seminis only in *Aploblema*, *Cephalogonimus* and in the distomes, and that on the basis of his own research Laurer's canal is wanting in *Monostomum mutabile*. One year later he states that in the monostomes a Laurer's canal appears to be wanting. Cohn (1902) reported the absence of both these organs in *Monostomum oculobium*. On the contrary Stossich in the same year after a thorough study of the group confirmed the presence of these organs in several species belonging to at least three genera of this family. Arnsdorff (1908) describes for *Monostomum vicarium* a small receptaculum seminis. Kossack (1911) after a study of a large number of specimens belonging to different genera of this family, viz: *Cyclocoelum*, *Typhlocoelum*, *Haematotrephus*, *Hyptiasmus*, states contrary to the finding of Stossich that both receptaculum seminis and Laurer's canal are wanting in this family. S. J. Johnston (1916) makes no mention of either the receptaculum seminis or Laurer's canal in any one of the three genera studied, *Cyclocoelum*, *Haematotrephus* and *Hyptiasmus*.

In a study of a considerable number of specimens belonging to several species of the genus *Cyclocoelum* the writer has observed the presence of the receptaculum seminis. In addition to the observations made on the American material the writer has been given the opportunity through the efforts of Professor Henry B. Ward and the courtesies extended him by the Curators of the museums of Berlin, Göttingen, and Vienna, to study *Cyclo-*

*coelum mutabile*, *Cyclocoelum problematicum*, *Cyclocoelum ovopunctatum*, *Cyclocoelum brazilianum*, *Cyclocoelum tringae*, and *Haematotrephus similis*. In all of these species a small spherical receptaculum seminis has been found, in position median and dorsal to the ovary (Figs. 20-24, 26 and 27).

On the same dorsal level with the receptaculum seminis and posterior to the latter and the ovary one finds the compact shell gland, in size approximately equal to the ovary. It is composed of unicellular glands closely packed together, each of which empties its secretion into the ootype by means of a short straight canal; these ducts form the inner portion of the gland. The ootype in the central portion of this gland gives rise to the uterus which in turn expands, immediately upon emerging, into a large receptaculum seminalis uterinum. During the sexual activity of the worm this pouch is filled with spermatozoa. In the genus *Cyclocoelum*, the uterus forms relatively short closely packed loops, in general going out from the middle line of the body. Relatively few stretches go directly across the body. The uterus fills out the entire space between the crura, then by a relatively straight stretch it spans the distance to the genital atrium in the region of the pharynx. In lateral extent the uterus reaches in general to the middle or outer wall of the intestine or rarely even out to the body wall, as in *Cyclocoelum halli*. This species differs in this respect from other species of the genus and according to the generic limits of Kossack does not belong here if this condition is a diagnostic factor. *Cyclocoelum halli*, however, conforms so closely to the genus in other respects and does not conform to the genus *Haematotrephus* in that the uterine loops do not bend around the genital organs so that the writer feels justified in placing it in the genus *Cyclocoelum*. Evidently there is little justification for the creation of a new genus based largely on the extent of the uterus and hence the limits of the genus *Cyclocoelum* have been extended to include this species.

The condition known as a situs inversus is a common feature of this family. Looss (1899) asserted that in all forms in which the genital pore is median there is a possibility that sexual amphitypy will occur and suggested that in Monostomes where this is the case situs inversus will probably be found. Cohn (1902) was the first to record this condition in the group when he found in *Spaniometra oculobia* (Cohn) a situs inversus of the genital glands in a ratio of 9:5. Kossack (1911) added to this by his observations on *Cyclocoelum problematicum* Stoss., *Cyclocoelum ovopunctatum* Stoss., and *Cyclocoelum vicarium* (Arnsd.) in which he says that on the average the right and left positions are equally frequently present.

The writer has found a similar condition to exist in all species of *Cyclocoelum* represented in North America as well as being able to verify the observations of Kossack on *Cyclocoelum problematicum* and *Cyclocoelum ovopunctatum*. Reference to the following table shows that the right and



left positions are on the whole equal in number and where significant differences occur they are perhaps due to the small number of individuals studied. In *Cyclocoelum obscurum* with sixty specimens in the lot the difference is relatively small. The total of ninety-four specimens in all show an approximately equal count for each arrangement.

	Anterior testis		Cirrus pouch		Number of uterine loops between testis									Total uterine loops on side of anterior testis					
	Rt.	Lt.	Rt.	Lt.	0	1	2	3	4	5	6	7	8	9	25-30	30-35	35-40	40-45	45-50
C. obscurum . . .	34	26	28	32	1	1	5	...	...	...	4	6	3	1	9	23	22	5	...
C. elongatum . .	4	4	3	4	...	...	...	...	1	5	1	1	...	...	...	...	2	3	2
C. pseudomicrostomum . . .	3	1	2	2	...	...	...	...	1	...	1	1	...	1	1	2	1	...	...
C. macrorchis . .	8	14	7	15	1	6	3	6	1	3	2	...	...	...	1	4	12	5	...
Total numbers .	49	45	40	54	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...

The variation in the position of the testes from one another is equally of little importance from the standpoint of specific diagnosis. However, since Stossich used this as the means of separation of species in *Cyclocoelum* and *Haematotrephus* the writer feels it worth while to give here the result of observations on American material. Kossack raised objections to the importance assigned this point by Stossich and showed that the variation within a species was even greater than that between the genera before mentioned.

The study of the American material has served to substantiate the view of Kossack (1911) reached by study of the European material. Reference to table shows the number of uterine loops to vary from none where the testes lie contiguous to one another to nine while the entire number of uterus loops, counted always on the side of the anterior testis, is likewise variable and appears to bear no relation to the total number of uterine loops between the testes of the individual since the specimen which showed nine loops between the testes has in all only 38 loops while in another individual of the same lot of *Cyclocoelum obscurum*, which had a total of 40 loops only 3 could be found between the testes. Other examples are 8 and 43; 3 and 44; 7 and 39 as compared to 1 and 39. These are a few examples taken from *Cyclocoelum obscurum*. Other species show the same to be true except in *Cyclocoelum halli* and *Cyclocoelum triangularum* where the relative positions of the genital glands appear to be constant. How-



ever, since the number of specimens here is small the writer is inclined to attach relatively little importance to this feature.

The life history of this group is relatively unknown, although the earliest record of a monostome larva is said to date from 1817. An early account is found in Filippi 1859. This author obtained from *Bythinia tentaculata* (L) [= *Paludina impura* of Filippi] a larva he named *Cerceria lophocerca* which he described (1859:5) as follows: "Elle est caractérisée par un bulbe pharyngien assez fort, par la présence de deux yeux ou taches pigmentaires semilunaires avec une petite lentille dans la concavité, et par une queue munie d'une crête membraneuse longitudinale. Dans l'intérieur du corps on voit des rudiments d'organes sexuels sous la forme de trois masses vésiculaires."

According to Lühe (1909) the determination of Filippi is doubtful since the description and figures show a close resemblance to *Cercaria fulvopunctata* Ercol. which is an undoubted distome larva. Cort (1915) on the other hand recognized distinct features in this larva and stated that it is "entirely different from all other monostomes known." As such it stands alone and unidentified.

While the description of Filippi is meager and bereft of many diagnostic characters a few outstanding features point to its alliance to this group. This relationship is shown by the absence or at most only poorly developed oral sucker (Filippi, pl. I, fig. 3), by the presence of a strongly developed pharynx, and by the position of the three "rudimentary" sex organs.

#### Key to species of *Cyclocoelum*

- 1(6) Uterus restricted to the intercecal zone ..... 2
- 2(5) Testes unequal in size ..... 3
- 3(4) Pharynx larger than oral sucker; ratio of posterior testis to ovary 2:1 ..... *Cyclocoelum mutabile* (Zed.)
- 4(3) Oral sucker and pharynx small, approximately equal in size; ratio of anterior testis to ovary 4:3 ..... *Cyclocoelum cuneatum* nov. spec.
- 5(2) Testes equal in size. Oral sucker larger than pharynx; ratio of testes too vary 3:1 ..... *Cyclocoelum leidyi* nov. spec.
- 6(1) Uterus not restricted to intercecal zone ..... 8
- 7(26) Uterus folding around the crura both dorsally and ventrally . . . 9
- 8(21) Genital glands separated by uterine loops ..... 10
- 9(16) Testes equal in size ..... 11
- 10(13) Pharynx larger than sucker; vitellaria extending laterally beyond medial wall of crura . . . 12
- 11(12) Ratio of testes to ovary 5:2 ..... *Cyclocoelum pseudomicrostomum* nov. spec.
- 12(11) Ratio of testes to ovary 4:3 . . . *Cyclocoelum microstomum* (Crepl.)

- 13(10) Sucker larger than the pharynx.....15
- 14(15) Vitellaria strongly developed, extending to inner wall of intestine; ratio of testes to ovary 2:1.....  
..... *Cyclocoelum macrorchis* nov. spec.
- 15(14) Vitellaria weakly developed, rarely reaching middle of crura; ratio of testes to ovary 2:1.....  
..... *Cyclocoelum vicarium* (Arnsd.)
- 16(9) Testes unequal in size.....18
- 17(20) Oral sucker twice as large as pharynx.....19
- 18(19) Ratio of posterior testis to ovary 2:1.....  
..... *Cyclocoelum obscurum* (Leidy)
- 19(18) Ratio of posterior testis to ovary 3:1.....  
..... *Cyclocoelum ovopunctatum* Stoss.
- 20(17) Oral sucker not twice the size of pharynx. Ratio of posterior testis to ovary 3:1..... *Cyclocoelum problematicum* Stoss.
- 21(8) Genital glands contiguous, not separated by uterine loops...24
- 22(25) Testes unequal in size; oral sucker twice as large as pharynx 25  
..... *Cyclocoelum wilsoni* nov. spec.
- 24(23) Ratio of posterior testis to ovary 2:1.....  
..... *Cyclocoelum tringae* (Brandes)
- 25(22) Testes equal in size; oral sucker and pharynx approximately equal. Ratio of testes to ovary 10:7.....  
..... *Cyclocoelum triangularum* nov. spec.
- 26(7) Uterus passing dorsally over intestinal crura and vitellaria to body wall; vitellaria moderately developed, rarely extending beyond middle of crura.....30
- 27(28) Sucker  $1\frac{1}{2}$  times pharynx; testes unequal; ratio posterior testis to ovary 3:2..... *Cyclocoelum brazilianum* Stoss.
- 28(29) Sucker and pharynx equal in size; testes equal; ratio of testes to ovary 2:1..... *Cyclocoelum halli* nov. spec.

*Description of species*

CYCLOCOELUM LEIDYI nov. spec.

[Figures 1, 2, 33]

Syn: *Monostomum mutabile* Leidy 1885, nec Zeder 1800

This collection contains five specimens described by Leidy (1885) as follows: "From the thoracic cavity of a Gray Snipe, *Gallinago wilsoni*, Dr. Warren (of Westchester) obtained five Flukes, 18mm long, by 4mm broad. These appear to be *Monostomum mutabile*."

These specimens are readily recognized as belonging to the genus *Cyclocoelum* Brandes (1892) but are distinctly different from *Cyclocoelum mutabile* and represent a new species. The following description shows the characteristic differences between the two species.

These flukes are 16 to 18 mm long by 4 to 4.5 mm broad. The margins of the body are practically parallel in the posterior two-thirds of the body. The anterior one-third tapers to a weakly rounded point. The subterminal mouth is surrounded by a weakly developed sucking musculature which is approximately three times the size of the small pharynx. The small ovoid pharynx measures  $231\mu$  broad by  $281\mu$  long. The slender esophagus which is curved in the form of an S measures  $331\mu$  in length. It opens into the middle of the dorsal side of the intestinal bifurcation. The voluminous intestinal crura run parallel to the margins of the body throughout their entire course. The vitellaria are moderately developed and occupy the region lateral to the crura. They extend laterally to the inner wall of the crura and fold both dorsally and ventrally around them. They extend anteriorly not quite to the most anterior portion of the intestinal bifurcation and are separated at the posterior end only by the excretory bladder. The uterus fills the entire space between the intestinal crura. It lies in the mid dorso-ventral region, is profusely coiled and does not extend out beyond the inner wall of the intestine. Genital glands are confined to the posterior intestinal arch. The posterior testis is situated in the middle line of the body and lies directly in the arch formed by the intestine. The anterior testis is a little removed and is contiguous to the crura. They are equal in size and measure 877 to  $910\mu$  in diameter. The much smaller ovary lies on the side of the body opposite to the anterior testis and in a transverse plane between the two testes. It is spherical and measures from 380 to  $390\mu$  in diameter. Dorsally and on the inner posterior side of the ovary is a small spherical receptaculum seminis 82 to  $99\mu$  in diameter, which joins by a short duct the oviduct shortly after its emergence from the ovary. Laurer's canal is not present. As the oviduct passes posteriorly into the adjacent shell gland aggregate it is joined by the vitelline duct. At this point the oviduct enlarges to form the ootype. Just after the uterus emerges from the compact shell gland a second enlargement is seen, the receptaculum seminalis uterinum. It extends posteriorly to the crura where it doubles on itself and pursues its coiled winding course to the genital pore which is situated ventral to the middle region of the pharynx. The cirrus pouch is  $182\mu$  broad by  $331\mu$  long and reaches to the middle of the intestinal crura at their bifurcation. The genital pores open separately into a small genital atrium. Eggs thick shelled ovals, 66 by  $117\mu$  when fully mature. They contain in the anterior portion of the uterus well developed miracidia as evidenced by the dark eye spots.

Habitat: Thoracic cavity

Host: *Gallinago wilsoni*

Locality: Westchester, Pa.

Date: 1885

Collector: Dr. H. W. Warren

No. 106 Leidy Collection.

A comparison of this material with the data given by Stossich (1902: 13) and by Kossack (1911:510) for *Cyclocoelum mutabile* (Zeder) as well as



comparison with specimens of *Cyclocoelum mutabile* obtained from the Göttingen museum demonstrates clearly that this is a distinct species. It is similar to *Cyclocoelum mutabile* in the size and form of the body, in the lateral extent of the uterine loops, the extent and development of the vitellaria, the size of the ovary, and the size and shape of the eggs.

It differs from this species in having a much smaller pharynx, a much larger sucker, a longer esophagus, larger testes, and a relatively heavier and more irregularly folded uterus. This species is similar to *Cyclocoelum problematicum* Stossich in the size of the testes and the extent of the vitellaria but differs from that species in having a smaller pharynx and a broader, thinner and less muscular body in proportion to its length. For comparison with this species a figure (Fig. 3) of *Cyclocoelum mutabile* (Zed.) is placed beside that of *Cyclocoelum leidyi*.

CYCLOCOELUM PSEUDOMICROSTOMUM nov. spec.

[Figures 4, 27, 30, 43]

Large monostomes 13 to 14.5 mm in length by 4 to 4.5 mm in greatest width which is found at the beginning of the posterior body third. From this point forward the side walls taper gradually to the end of the anterior body third, at which point they bend inwardly more sharply to form a small obtusely rounded end. The posterior end is bluntly rounded. The mouth is subterminal, surrounded by an external banding musculature which measures 662 to 745 $\mu$  in diameter. This is followed by a large heavy slightly elongate pharynx 778 to 910 $\mu$  in length by 745 to 844 $\mu$  in width. The genital pore lies median and ventral to the forward end of the pharynx. From this point the cirrus pouch stretches posteriad almost to the posterior wall of the intestinal bifurcation. The vitellaria extend from the posterior end of the cirrus pouch to the excretory bladder in the posterior end of the body. It is even more strongly developed than that of *Cyclocoelum microstomum* and in its lateral extent passes the inner wall of the crura and over the lateral folds of the uterine loops which in this species rarely pass over the inner wall of the crura. The testes as in other species of this genus lie in the posterior region of the body and within the intestinal crura. The posterior testis does not fill the entire intestinal arch, is antero-posteriorly flattened and measures 827 to 910 $\mu$  in width by 993 to 1192 $\mu$  in length, while the anterior testis which is separated from it by uterine loops measures 745 to 993 $\mu$  in width by 1076 to 1324 $\mu$  in length. The ovary lies on a level with the anterior margin of the posterior testis and adjacent to the cecum opposite to the anterior testis, is much smaller and spherical, measuring 413 to 496 $\mu$  in diameter. Dorsal to the ovary is the spherical receptaculum seminis 148 to 165 $\mu$  in diameter. The shell gland is similar in size to the ovary and occupies a position dorsal and posterior to that structure. As was stated above the uterus does not usually pass over the



inner wall of the intestine and fills out entirely the space between the crura. The eggs are thick shelled ovals, 51 to 66 $\mu$  in width by 102 $\mu$  in length.

Habitat: Lung

Host: "Wild duck"

Locality: Omaha, Nebr.

Date: 1903

Collector: C. E. Stringer

No. 1041 Ward Collection

This species is also found in the Leidy Collection vial no. 186 which has been dried out and is in a poor state of preservation. John C. Johnson collected this species from *Fulica americana* taken at Golden Gate Park, San Francisco, Cal. in January 1919.

*Cyclocoelum pseudomicrostomum* finds its nearest relative in *Cyclocoelum microstomum* (Crepl.). The two species are of nearly equal size. The pharynx of the former is distinctly larger, the testes are not of equal size as in *C. microstomum* and are slightly broader than long probably due to pressure from the closely packed uterus. The ovary of *Cyclocoelum pseudomicrostomum* is noticeably smaller than that of *Cyclocoelum microstomum*, while the lateral extent of the uterus in the former species is more restricted. With respect to the development of the vitelline glands *Cyclocoelum pseudomicrostomum* presents the heaviest development found in any known species of this genus.

#### CYCLOCOELUM HALLI nov. spec.

[Figures 5, 11, 20, 36-42]

Large monostomes varying in length from 11 to 14 mm in width by 3 to 4 mm in greatest width which is found slightly posterior to the middle of the body. From this point the body tapers anteriorly to almost a point and posteriorly only a little, forming an obtusely rounded end. The body is muscular, dorsally convex, and ventrally flat or slightly concave. The body wall is entirely covered with numerous small pits observed by Zeder (1803) in *Monostoma mutabile*. The subterminal mouth leads by a funnel-shaped tube to the pharynx. This tube or mouth proper is surrounded by a concentration of musculature which on the outer margin is formed into circular bands, the outer covering of the sucker (Figs. 36 to 42). The sucker is spherical in form and measures 387 $\mu$  in diameter. It is separated from the smaller (263 $\mu$ ) but more heavily muscular, spherical pharynx, by the nerve commissure. The esophagus is 483 $\mu$  in length and extends from the posterior portion of the pharynx to the dorsal side of the intestinal bifurcation. The latter a simple tubular structure lies along the margins of the body for its entire length and anastomoses at the posterior end. As previously described the excretory system is composed of a system of tubules ramifying the entire body in this species, as in *Cyclocoelum elongatum*. These tubules anastomose and empty into the excretory bladder. In this species a single thin walled sac

which opens to the exterior by a small dorsal pore. The genital glands are situated in the posterior fifth of the body where they are closely packed in the posterior arch of the intestine, the posterior testis almost entirely filling this space. It is slightly flattened antero-posteriorly and measures in its greatest dimension  $1052\mu$  and in an axis at right angles to this,  $894\mu$ . The anterior testis situated a short distance cephalad to the posterior, is spherical in shape and a little smaller, having a diameter of  $894\mu$ . The two testes are separated by a particularly long loop of the uterus which extends to the intestinal arch, and in some instances even beyond, and usually folds back part way forming a double loop. The vasa efferentia given off from the anterior margins of the two testes unite cephalad and mesad to the anterior testis to form the vas deferens which takes a fairly straight course to the cirrus pouch with which it unites.

The cirrus pouch is a rather large oblong sac extending from the pharynx to a short distance beyond the anterior wall of the intestinal bifurcation. It opens into a small genital atrium which in turn opens to the exterior, ventral to the pharynx.

The ovarian complex is situated opposite to and on a level with the anterior testis. The ovary is very much smaller than the testes, measuring  $434\mu$  in diameter. Dorsal to this is the receptaculum seminis, the duct from which joins the oviduct before it enters the shell gland. The shell gland, a compact spherical organ, is situated dorsal and posterior to the ovary. It has a diameter of  $388\mu$ . The vitellaria lie between the lateral body wall and the external wall of the digestive crura over which they seldom pass. They extend from the posterior pharyngeal region to the extreme posterior end where they are separated by the excretory bladder. The vitelline glands are made up of small follicular grape-like clusters arranged along a main stem, which in the region of the anterior testis gives rise to the vitelline ducts. These pass mesad and unite a short distance posterior to the shell gland to form the common duct which passes straight to the shell gland. It enters this at the posterior side and passes through the outer portion of this organ to its union with the oviduct just after the entrance of the latter into the shell gland. The oviduct then enlarges to form the ootype. On emergence from the shell gland the uterus enlarges to form a large pouch, the receptaculum seminalis uterinum. From this the uterus makes a few short loops and then the long loop, previously mentioned, which separates the testes. From this point forward it lies in more or less regular transverse folds which extend out to the vitellaria, tho in some instances, particularly in the posterior three-fifths of the body, these loops extend to the body wall. In the anterior fifth of the body the uterine loops are not so long and here fill out entirely the space between the intestinal crura. From the

bifurcation of the intestine the uterus reaches in a relatively straight stretch to the genital atrium.

The eggs are large, thick shelled ovals, measuring  $161\mu$  in length by  $99\mu$  in breadth. The double, dark eyespots give evidence of the developing miracidium within the eggs before they have passed in their course anterior to the middle region of the body.

Habitat: Abdominal air-sacs.

Locality: host taken in Raleigh  
(?) N. C.

Host: *Totanus melanoleucus*

Date: April 7, 1894

Collector: W. C. Hall

No. 21.90 Ward collection

Habitat: Liver? or Lung?

Locality: Creston, Iowa

Host: *Totanus solitarius*

Collector: W. C. Hall

Date: Aug. 30, 1895

No. 21.763 Ward collection

Filed among the records of Hall is a statement that he collected 5 specimens from the air sacs of *Totanus flavipes* Sept. 4, 1895, which he believed to be this species. The material from this host has not been found.

This species is most closely related to *Cyclocoelum brazilianum* Stossich and resembles that form in the lateral extent of the uterus, the relative position of the genital glands, and in the size of the ovary. It differs, however, in the size of the testes, the more weakly developed vitellaria, and relative size of the oral sucker and pharynx, these being of equal size in *C. halli* while in *C. brazilianum* the sucker is distinctly larger than the pharynx.

#### CYCLOCOELUM WILSONI nov. spec.

[Figure 6]

Medium sized monostomes 12 mm long by 3 mm wide in maximum which is found at the beginning of the posterior one-fifth of the body. Posterior and bluntly rounded. Anterior to the point of greatest width the body tapers gradually to a blunt but relatively small point. The mouth sucker measures  $374\mu$  in diameter and is one-third larger than the oval pharynx which measures  $298\mu$  in length by  $269\mu$  in width. The esophagus is relatively long and gives rise by bifurcation to the simple intestinal crura, which as in other species run parallel to the body wall and anastomose in the posterior end of the body. The genital aperture is ventral to the middle of the pharynx. The cirrus pouch extends from this point to the middle of the intestinal bifurcation. The follicular yolk glands extend from the anterior wall of the intestinal bifurcation almost to the excretory bladder at the posterior end. In lateral expanse they pass over the external wall of the intestinal crura to the middle of that organ where they meet the furthest expanse of the uterus. The uterus in this species lies entirely anterior to the anterior testis and fills out the space between the crura, folding both dorsally and ventrally over the walls of



these to the middle region of the same. The genital glands lie contiguous to one another in the posterior arch of the intestine. The posterior testis lies a little posterior to and a little more nearly in the middle of the arch than the anterior one which is smaller and contiguous to the former, filling out the opposite portion of the intestinal arch. The testes are not separated by uterine loops as is generally true in this genus. The anterior testis is spherical,  $910\mu$  in diameter while the posterior testis is slightly elongated and measures  $993\mu$  in length by  $910\mu$  in width. The ovarian complex lies anterior to and adjacent to the posterior testis. The ovary and shell gland are spherical, equal in size, and measure  $413$  to  $447\mu$  in diameter. The small spherical receptaculum seminis lies partially embedded in the shell gland and measures  $150\mu$  in diameter. The eggs are thick shelled ovals and measure  $150\mu$  in length by  $76\mu$  in width.

Habitat: Intestine

Host: *Gallinago wilsoni*

Locality: Creston, Iowa

Date: August 4, 1894

Collector: W. C. Hall

No. 21.89 Ward Collection

The direct relationship of this species is not so readily apparent. As to position of the genital glands it holds a place close to *Cyclocoelum tringae* (Brandes) and *Cyclocoelum triangularum* nov. spec. and tho it is much larger presents in general the same characteristic features namely: genital glands contiguous, uterine loops directed backward, vitellaria moderately deveoped, oral sucker larger than pharynx. However, in the size of the body and the relative size of the pharynx and sucker as well as the relative size of the genital glands *Cyclocoelum wilsoni* is clearly distinct and must be recognized as a proper species.

#### CYCLOCOELUM CUNEATUM nov. spec.

[Figures 7, 24]

Medium sized worms  $10.5$  to  $12$  mm in length by  $2.5$  to  $3.5$  mm in greatest width which is found at the beginning of the posterior body fourth. From the point of maximum width the margins of the body run approximately parallel to the level of the anterior testis at which point they narrow abruptly to form the obtusely rounded posterior end. From the point of greatest width the margins of the body converge cephalad in almost straight lines to a very narrow and pointed anterior end, which gives the impression of a well formed wedge. At the pointed anterior end is found a very small weakly developed sucker,  $198$  to  $215\mu$  in diameter. This is followed by an oblong pharynx of approximately the same width as the sucker. It measures  $150$  to  $198\mu$  in width by  $215$  to  $231\mu$  in length. The esophagus is three and one-half to four times the length of the pharynx. The intestinal crura are simple. The vitelline glands extend from the middle region of the bifurcation of the intestine to the excretory bladder



in the posterior end. In lateral extent they rarely traverse the outer wall of the crura. The genital opening is located anterior to the pharynx. The cirrus pouch extends to the anterior wall of the intestinal bifurcation. The uterus fills out the entire space between the crura and its loops occasionally span the outer wall of the same organ. The genital glands are relatively small and occupy the positions so common to the species of this genus. The posterior testis, not filling out the intestinal arch, is antero-posteriorly flattened and measures  $413\mu$  in width by 496 to  $612\mu$  in length. The anterior testis is separated from the posterior by several uterine loops and is smaller and spherical, measuring 331 to  $413\mu$  in diameter. The spherical ovary is situated in a transverse plane anterior to and about equally distant from the two testes. It is one-fourth smaller than the testes measuring 215 to  $331\mu$  in diameter. The shell gland lies median and posterior to the ovary, is spherical or only slightly ovoid and equal in size to the latter organ. The receptaculum seminis although indistinguishable in toto mounts is clearly seen in sections. It is anterior and dorsal to the ovary. Wax reconstructions show it to be spherical and approximately one-half the size of the ovary, measuring  $150\mu$  in diameter. The ovarian complex is separated from the testes by uterine loops. The eggs are thick shelled ovals,  $66\mu$  wide by  $115\mu$  to  $122\mu$  long.

Habitat: Abdominal cavity

Host: *Gallinago delicata* (Ord.)

Locality: ?

Date: ?

Collector: ?

No. 08. 172 Ward collection.

The relationships of this species is not so evident as it partakes of the characteristics of a number of species. With respect to the lateral extent of the uterine loops it is more nearly like *Cyclocoelum mutabile* and *Cyclocoelum leidy* while in development of the vitellaria it simulates *Cyclocoelum halli*. The pharynx and oral sucker are noticeably smaller than in any known species of this genus and this is a feature of this species as is also the small size of the genital glands and the proportionate size of the testes to the ovary, a ratio of 4:3.

### CYCLOCOELUM OBSCURUM (Leidy)

[Figures 8, 21]

Syn: *Monostomum obscurum* Leidy 1887

This species was described by Leidy as follows: "Elongated, elliptical, flattened, obtusely angular in front, obtusely rounded behind, oral and genital and other apertures scarcely distinguishable. Length 4 to 8 lines; width 1 line."

"Numerous specimens in the stomach of a Jew-fish, *Megalops thrissoides*."

The host name *Megalops thrissoides* used for the Jew-fish by Leidy 1887 is evidently a *lapsus calami*. However this is corrected by Stiles and Hassall (1894) to *Stereolepis* sp?

Brandes (1892) enumerates this among other species which he has not had opportunity to study and he justly says that it is inadequately described. Monticelli (1892) and Braun (1893) in spite of the meager description retain it as a valid species.

The original material of this species is found in the Army Medical Museum under Number 1035 Comparative Anatomy Series with the description "Flukes *Monostomum obscurum* from the stomach of a Jewfish (*Stereolepis*)."

From this I have written the following description.

Monostomes of medium size measuring from 6 to 13 mm in length and from 1.5 to 3 mm in maximum width which is found a little posterior to the middle of the body. The margins of the body are almost parallel for the greater part of their length, tapering gently to the more pointed anterior end and abruptly to form the obtusely rounded posterior end. As in most species of this genus the body is convex dorsally and flat or slightly concave ventrally. The subterminal mouth is surrounded by a weakly developed sucking musculature which measures  $115\mu$  in diameter. This leads to the spherical or slightly elongated pharynx, measuring  $115$  to  $264\mu$  in width by  $115$  to  $298\mu$  in length. Following this the slender esophagus,  $500$  to  $750\mu$  in length, leads to the intestinal bifurcation. The crura are quite variable in size as well as in the character of the median wall. In some cases they show a tendency to the formation of internal ceca; these appear to be due to the pressure from the closely packed uterus which fills the space between the crura. The excretory system in this species has not been made out except for the single terminal excretory vesicle situated as in the other species of this genus between the posterior arch of the intestinal crura and the posterior body wall. It opens to the exterior by a single dorsal pore. The genital organs lie within the intestinal crura in the posterior end of the body. The posterior testis, filling the posterior arch of the intestine, is flattened anteriorly by the closely packed uterine loops and is slightly larger than the anterior being  $300$  to  $877\mu$  in width by  $480$  to  $1000\mu$  in length. The anterior testis is usually more nearly spherical and measures  $380$  to  $827\mu$  in width by  $462$  to  $827\mu$  in length. It lies obliquely anterior to the posterior and adjacent to the crura. The vasa efferentia are short and unite a short distance anterior to the anterior testis to form the vas deferens which for the most part passes dorsal to the uterus to the cirrus pouch. This organ is of medium size  $248$  to  $579\mu$  in length by  $115$  to  $199\mu$  in width. In general its posterior limit lies on a level with the middle of the intestinal bifurcation. The ovarian complex lies between the testes and on the side opposite to the anterior testis. It is composed of a spherical ovary,  $275$  to  $463\mu$  in diameter, a spherical receptaculum seminis,  $132$  to  $148\mu$  in diameter, and a shell gland in size and form similar to the ovary. The position of these is clearly shown in figure 21. Beginning in the shell gland the uterus immediately upon

emergence enlarges to form the large receptaculum seminalis uterinum. It fills the intercecal space with more or less regular loops which in general go out from the middle of the body. These loops fold around the inner surface of the crura and usually do not pass beyond the outer wall of the latter organ. The vitellaria for the most lie outside the crura and extend from the pharynx to the excretory bladder. Laterally they reach to the middle of the crura and in exceptional instances to the inner wall of that organ.

Habitat: Stomach

Host: *Stereolepis* sp?

Locality: ?

Date: ?

Collector: ?

Cat. No. 1035 Comparative Anatomy series.

Habitat: ?

Host: *Symphaemia semipalmata*

Locality: Lincoln, Nebraska

Date: ?

Collector: ?

Cat. No. 08.179 Ward collection

Habitat: ?

Host: Unknown

Locality: Spokane, Wash.

Date: ?

Collector: W. E. Allen

Cat. No. 08.183 Ward collection

*Cyclocoelum obscurum* is most closely related to *Cyclocoelum ovopunctatum* Stossich and differs from that species in the more slender form, the more heavily developed vitellaria and the relative size of the testes to the ovary which in *Cyclocoelum obscurum* are twice as large as the ovary while in *Cyclocoelum ovopunctatum* they are three times as large.

#### CYCLOCOELUM MACRORCHIS nov. spec.

[Figure 9]

This species varies in length from 7 to 15 mm and in maximum width, which is found just posterior to the middle of the body, from 2 to 4 mm. From this point the body tapers towards both ends, the posterior being obtusely rounded while the anterior is considerably more attenuated. It forms a moderately rounded point. The margins of the body lie nearly parallel in the middle region of the body. The subterminal mouth is surrounded by a weakly developed musculature, the oral sucker, which is only a little larger than the well developed pharynx just posterior to it, and measures  $255\mu$  in diameter. The pharynx is oval in shape being about one-fifth longer than wide and measures on the average  $271\mu$  long and  $238\mu$  wide. The esophagus in this species is on the whole well extended and ranges from  $331\mu$  in the state of least extension to  $662\mu$  in that of greatest extension exhibited in preserved material. At its posterior end the esophagus turns ventrad and bifurcates forming the voluminous crura present in this species (Fig. 9). These as in other species of this genus lie parallel to the margins of the body and anastomose at the poster-



ior end. The excretory system as far as can be made out in preserved material conforms in this species to the description given previously in having a single thin walled vesicle in the extreme posterior end of the body into which the anastomosing tubules empty. It opens to the exterior slightly dorsal to the posterior end. The genital glands in general occupy the intercecal zone and fill entirely that space. The posterior testis occupies the intestinal arch, is usually spherical in form and measures 783 to 984 $\mu$  in diameter. The anterior testis is usually removed from the posterior by several uterus loops. It is spherical and approximately the same size as the posterior measuring 730 to 860 $\mu$  in diameter. As in other species of this genus the vasa efferentia unite cephalad and mesad to the anterior testis. From this point the vas deferens takes its course among the uterine folds to the posterior end of the cirrus pouch which is situated at the middle of the intestinal bifurcation. The cirrus pouch extends from the genital atrium caudad to the middle of the intestinal bifurcation. From this point the club-shaped cirrus pouch extends cephalad to the genital atrium and lies ventral to the anterior end of the pharynx. The ovarian complex is situated between the testes and adjacent to the crura opposite the anterior testis. The ovary is spherical and measures 413 to 463 $\mu$  in diameter. Dorsal and posterior to the ovary is the spherical receptaculum seminis, 165 $\mu$  in diameter. The duct of this unites with the oviduct before it enters the shell gland. The shell gland is approximately the same size as the ovary and is situated posterior and dorsal to that organ (Fig. 9). The well developed follicular yolk glands occupy the region of the body lateral to the intestinal crura and extend from the anterior-most part of the intestinal bifurcation to the posterior end where they are separated only by the small excretory bladder. The follicles are arranged in clusters on secondary branches from the main stem and in this manner extend laterad around the crura both dorsally and ventrally, in many cases reaching out as far as the inner wall of the crura. The vitelline ducts are given off in the region of the shell gland and pass mesad to a point just dorsal to the shell gland where they unite to form the vitelline reservoir. From this the common vitelline duct passes dorsal to the shell gland and joins the oviduct just before its entrance into that organ. Immediately upon entering the shell gland the oviduct enlarges to form the ootype. Upon emergence from this the uterus enlarges to form the receptaculum seminalis uterinum. From this point the much folded uterus fills out the entire space between the crura and passes over the bifurcation in a relatively straight stretch to the genital atrium. The numerous eggs which fill the uterus are thick shelled ovals, measuring from 122 to 153 $\mu$  in length by 56 to 66 $\mu$  in width. In general the eggs are smaller in the beginning of the uterus than they are near the genital orifice. The eggs in the anterior region show well developed miracidia with double dark eye spots.



Habitat: In lung and along the  
back in the abdomen.

Host: Straight-billed Curlew

Collector: W. E. Allen

No. 08.180 Ward collection

*Cyclocoelum macrorchis* differs from *Cyclocoelum mutabile* in that the uterus in the former is not restricted to the intercecal space and that the oral sucker is larger than the pharynx, where as in *Cyclocoelum mutabile* the vitellaria are more heavily developed and the genital glands are smaller. *Cyclocoelum macrorchis*, however, has a much more muscular and much thicker and heavier body.

#### CYCLOCOELUM TRIANGULARUM nov. spec.

[Figure 10]

Medium sized worms 8 mm long by 2.5 mm wide in maximum. Body lanceolate in form. Oral sucker weak,  $260\mu$  in diameter, only a little larger than the pharynx which is longer than broad, measuring  $248\mu$  in length by  $215\mu$  in breadth. The length of the esophagus is approximately one-tenth of the entire body length. Intestinal crura simple. Genital pore ventral to the posterior end of the pharynx. Cirrus pouch extending to the middle of the intestinal bifurcation. The vitellaria extends from the posterior end of the cirrus pouch almost to the excretory bladder at the posterior end of the worm. In lateral extent they pass over the wall of the crura to the middle of that organ. The genital glands lie in the posterior arch of the intestine and are not separated by uterine loops. The two testes lie on the same level, one in either side of the arch, are spherical and equal in size. They measure  $413\mu$  in diameter. The ovary lies anterior to the testes and in the middle line of the body. It is a little more than one-half the size of the testes, is spherical in form and measures  $248\mu$  in diameter. The shell gland lies between the ovary and testes also in the middle line of the body and measures  $264\mu$  in width by  $314\mu$  in length. The receptaculum seminis is situated anterior to the shell gland and dorsal to the ovary. Like the ovary the receptaculum seminis is spherical in form and measures  $132\mu$  in diameter. The eggs are thick shelled ovals  $132\mu$  long by  $75\mu$  wide.

Habitat: Abdominal air sacs

Host: *Tringa maculata*

Locality: Creston, Iowa

Date: September 4, 1895

Collector: W. C. Hall

No. 21.88 Ward collection

As was stated in another section of this paper *Cyclocoelum triangularum* shows a striking similarity to *Cyclocoelum wilsoni* and is distinguished from that species by the generally smaller body, the more nearly equal sucker and pharynx, the testes of equal size and the relative size of the testes and ovary which in *Cyclocoelum triangularum* have a ratio of 10:7. It is more nearly equal in size with *Cyclocoelum tringae* but is distinguished from

this species by the larger pharynx, smaller sucker, the testes being equal in size and also smaller in proportion to the size of the ovary.

### CYCLOCOELUM VICARIUM (Arnsdorff 1908) Kossack 1911

Syn: *Monostomum vicarium* Arnsdorff

The writer has not had opportunity to study specimens of this species and hence must rely upon the descriptions of Arnsdorff (1908) and Kossack (1911). Since the description of Kossack made after having studied the original material is at variance with the original description only in minor detail the writer has based the following description on the work of Arnsdorff.

Monostomes varying between 10.5 and 14.4 mm in length and 3 to 3.1 mm in maximum breadth. The body is opaque, flattened; ventral surface flat, dorsal slightly swollen. The sidelines of the body diverge from the small pointed anterior end to the height of the testes. From here they form the bluntly rounded posterior end. The dorsal surface of the body is quite wrinkled. These folds appear in optical section to form papillae. The mouth opening is terminal. The strongly muscular pharynx is an elongate oval with a long diameter of  $460\mu$  and a breadth of  $270\mu$ . The thickness of its wall is  $130\mu$ . The esophagus,  $640\mu$  long, leads to the intestinal crura which run parallel to the side walls of the body and anastomose in the posterior end. The genital organs lie in the broad hinder end. The posterior testis is flattened antero-posteriorly and measures  $1190\mu$  in length by  $732\mu$  in breadth. It lies in the middle line of the body with its forward margin reaching to the vitelline duct. The anterior testis is spherical in form with a diameter of 835 to  $878\mu$ . It is removed anteriorly from the posterior end and lies adjacent to the intestinal crura. The ovary lies adjacent to the crural wall, opposite to the anterior testis and between the positions of the testes. It is spherical and has a diameter of  $402\mu$ . Between it and the posterior testis is found the relatively small receptaculum seminis.

The vitellaria are composed of numerous follicles which lie parallel to the body wall and between that and the intestinal crura; they extend from the region of the intestinal bifurcation to the posterior end where they are separated by a short interval. The numerous transverse uterus loops fill out the space between the crura and in the posterior half of the body overlap them. The genital pore is situated just posterior to the pharynx. The club-shaped cirrus pouch is small and does not reach the intestinal bifurcation. The eggs are numerous, elliptical in form and measure  $102\mu$  in length and  $68\mu$  in breadth. The ripe eggs hold a well developed embryo as can be recognized by the black eye spots in the miracidium.

The comparison of Arnsdorff with the figures and description of Stosich for closely related species show a striking similarity to *Cyclocoelum problematicum*. *Cyclocoelum vicarium* differs from this species, however, in the relative size of the worms, the extent of the cirrus pouch and the size of the eggs.

Habitat: Intestine

Host: *Arquatella maritima maritima*

Locality: North East Labrador

Date: September 14, 1906

Collector: Hantzsch

Königsberg Museum

#### NOTOCOTYLIDAE Lühe 1909

Of the monostome families which have up to this time been widely studied no other family is of greater interest than the Notocotylidae. It is in this family that the earliest records of the monostomes are found in *Catatropis verrucosa* (Frölich 1789) collected from the rectum of *Anas domestica*. These worms were classed by Frölich and Gmelin as *Fasciola*. Ten years later Zeder (1800) removed them to the genus *Monostoma*. They were later separated from the remaining monostomes by Diesing (1839) and placed in a new genus *Notocotylus* which genus remains as the type of the family. Although Diesing included this earliest known form in his genus *Notocotylus*, it has been found in more recent time by Odhner (1905) to be distinct from the Diesing type species, *Notocotylus triserialis*, and was removed to the new genus *Catatropis* which place it holds at present as type of that genus. A further study of *Notocotylus triserialis* Diesing by Kossack (1911) revealed its identity with *Monostomum attenuatum* Rud. 1809. Thus the species name becomes a synonym to *Notocotylus attenuatus*.

In regard to the early records of this family in America there still remains a question. Some authors notably Barker and Laughlin would place *Monostomum affine* Leidy 1858 as the earliest American record while others doubt this determination and still others reserve opinion on the matter. Barker (1916) questions the determination of Leidy and expresses the opinion that *Monostomum affine* Leidy belongs to the genus *Notocotylus*. While the description of Leidy (1858:110–112) is insufficient for an accurate determination of the systematic position of this species certain facts given in his description are distinct and seem sufficient to show that this worm is not Notocotylid in character. The length of *Monostomum affine* as given by Leidy is  $6\frac{1}{2}$  lines or 13.5 mm which is two and one-half to three times longer than any known species of this family. Likewise on the same basis the Leidy species is at least three times wider than the largest known Notocotylid. However, more important, intrinsic characters are the presence of a pharynx, an echinate penis and eggs prolonged at one pole only. In addition these worms were taken from the gall-bladder



and bile ducts of the muskrat while the Notocotyliidae are normally inhabitants of the intestine and rectum. It is not impossible that a Notocotylid species may have ascended the gall-duct of this host and become modified and adjusted to the new conditions. Yet on the basis of the facts noted above the writer cannot agree with the opinion of Barker regarding the Notocotylid character of these worms.

More recently Hassall (Stiles & Hassall 1894) collected from *Arvicola riparius* and *Fiber zibethicus* taken in Maryland in 1892 specimens determined as *Monostomum* sp. and one year later from *Aix sponsa* and *Dafila acuta* worms also determined as *Monostomum* sp. On observation and study by the writer the specimens taken from *Aix sponsa*, *Dafila acuta* and *Fiber zibethicus* have been found to be distinctly different from forms previously described and on the basis given in a later section must be recognized as a new species. On account of the similarity to the immature stages of *Cercaria urbanensis* Cort it is believed to be the adult form of this species. The material taken from *Arvicola riparius* has been found to agree with *Notocotylus quinqueserialis* (Barker and Laughlin 1911). Other American records are those of Barker (1915, 1916) in which he records *Catatropis filamentis* from *Fiber zibethicus* taken in Nebraska and *Nudocotyle novicia* from the same host taken in the same region.

Additional records presented in this paper are *Notocotylus urbanensis* (Cort 1914) from the black and domestic swan taken at Golden Gate Park, San Francisco, California by John C. Johnson in February 1919 and *Paramonostomum echinum* nov. spec. from the intestine of *Fiber zibethicus* taken at Wray, Colorado by C. H. Gable, October 1916.

DIAGNOSIS OF FAMILY

Small monostomes tapering at both ends, posterior end broadly rounded, anterior slightly more attenuated. Generally with rows of papillae formed of unicellular dermal glands. Esophagus short, without pharynx; intestinal ceca with short diverticula, extending entire length of body. Genital pore median, except in *Nudocotyle* where it is distinctly lateral, usually near oral sucker. Cirrus sac elongate. Testes symmetrical, extracecal, near posterior end. Ovary between testes. Vitellaria lateral, anterior to testes. Uterine coils between cirrus sac and genital glands, transverse, regular, usually not extending outside intestinal crura. Eggs small with long polar filament on each end.

KEY TO SUBFAMILIES AND GENERA

- 1(5) Genital pore anterior median...Sub-family Notocotylinæ..2
- 2(5) With ventral glands.....3
- 3(4) Ventral glands protrusible.....*Notocotylus* Diesing 1839
- 4(3) Ventral glands not protrusible.....*Catatropis* Odhner 1905



- 5(2) Ventral glands wanting . . . . . Paramonostomum Lühe 1909  
 6(1) Genital pore marginal posterior without ventral glands . . .  
 . . . . . Sub-family Nudocotylinæ . . 7  
 Uterus in anterior body half . . . . . Nudocotyle Barker 1916

The Notocotylidae are up to the present represented in North America by two species of *Notocotylus* and one species of each of the other genera in this family.

The Notocotylidae were subdivided by Kossack (1911) into two sub-families; Notocotylinæ including *Notocotylus* Diesing (1839) *Catatropis* Odhner (1905) and *Paramonostomum* Lühe (1909), and *Ogmogasterinae* represented by a single species *Ogmogaster plicatus* (Creplin 1829) Jägerskiöld 1891. A third subfamily Nudocotylinæ was created by Barker (1916) to hold *Nudocotyle novicia*. In this Barker would include *Barisomum erubescens* Linton (1910).

#### NOTOCOTYLINÆ Kossack 1911

Small to medium sized Notocotylidae with thin cup-shaped body; two to five rows of prominent papillae on ventral surface. Genital pore median, near intestinal bifurcation. Cirrus pouch enclosing only a small part of seminal vesicle. Vitellaria well developed occupying a region posterior to middle portion of body anterior to testes and lateral to intestinal crura. Ovary and testes symmetrical, in extreme posterior part of body. Ovary between testes and separated from them by intestinal crura. Uterus regularly coiled, between intestinal crura.

Type genus *Notocotylus*. Other American genera *Catatropis* and *Paramonostomum*.

#### NOTOCOTYLUS Diesing 1839

Syn: *Notocotyle* Diesing 1850

The genus *Notocotylus* was formed by Diesing in 1839 to include *Fasciola verrucosa* Frölich, *Fasciola anseris* Gmelin, *Festucaria pedata* Schrank and *Monostoma verrucosum* Zeder. It was characterized by the author as follows: "Corpore oblonga-ovato, depressiuscula, antice parum attenuato, postice rotundato, ore terminali orbiculari; acetabulis suctoriis dorsalibus numerosis, serie triplici longitudinali; cirro longo spirali ventrali." In 1850 the author changed the name to *Notocotyle* with only a slightly modified diagnosis as follows: "Corpus oblongum depressum. Caput corpore continuum. Os subterminale anticum. Acetabula numerosa (24-50) juxta totam dorsi convexiusculi longitudinem treseriata sissilia, orbicularia, limbo callosa. Penis ventralis superus longi spiralis. Porus excretorius . . . . In avium intestinis crassis et coecis endoparasita!" Under this caption Diesing included his former genus *Notocotylus*. Altho Monticelli, Barker and others adhere to the more recent form of the name

the writer feels justified under Article 32 of the International Rules of Zoological Nomenclature in accepting with Kossack, Ward and others the older name *Notocotylus*.

This genus is up to the present represented in America by a single species *Notocotylus quinquesequalis* (Barker and Laughlin). Altho Barker (1916) would place *Monostomum affine* Leidy in this group, his determination seems to be unwarranted on the basis of the description of Leidy which shows distinct anatomical differences namely a small pharynx, echinate penis, a well marked excretory canal traceable to the beginning of the oviduct, and sub-pyriform eggs prolonged at one pole only. In addition to the anatomical differences *Monostomum affine* was found parasitic in the gall bladder and gall ducts of *Fiber zibethicus* whereas *Notocotylus* has been taken only from the intestine and ceca of the muskrat and water birds.

#### NOTOCOTYLUS URBANENSIS (Cort 1914)

[Figures 12, 14, 17, 18, 19]

Syn: *Monostoma* sp. Stiles and Hassall 1894

Medium sized worms 2.5 to 3.5 mm long by 0.5 to 1 mm wide, having three rows of ventral glands each row containing 13 to 14 glands. Oral sucker strongly muscular 112 to 153 $\mu$  followed by a short esophagus without pharynx; intestinal crura provided with numerous short diverticula both externally and internally. Genital pore just posterior to intestinal bifurcation. From this point the cirrus pouch extends caudad to the end of the first body third or a little beyond this level. Vagina one-half the length of the cirrus. Usually about ten uterine loops anterior to the most anterior part of the vitellaria which as in other species of the genus lie lateral to the ceca and extend from the middle of the body to the lobed testes in the posterior end. The irregularly lobed ovary is situated between the testes and is separated from them by the crura. Eggs numerous possessing two long polar filaments. Eggs without filaments measure 20 $\mu$  in length, and are approximately one-half that in width.

Habitat: Intestine  
Locality: Maryland  
Date: January, 1893

Host: *Dafila acuta*  
Collector: A. Hassall  
No. 5772 U.S.N.M.

Habitat: Cecum  
Locality: Maryland  
Date: June 23, 1892

Host: *Fiber zibethicus*  
Collector: A. Hassall  
No. 5769 & 5770 U.S.N.M.

Habitat: Intestine  
Locality: Maryland  
Date: August, 1893

Host: *Aix sponsa*  
Collector: A. Hassall  
No. 5771 U.S.N.M.

*Notocotylus urbanensis* agrees with *Notocotylus attenuatus* in size and form, and in the relative length of the cirrus pouch and vagina. With respect to the number of papillae in each row it conforms more closely

to *Notocotylus aegyptiacus*; it differs, however, from this species in the relative length of the cirrus pouch and vagina. In the position of the genital pore it agrees with *Notocotylus seineti* Fuhr. and in this respect it differs from other known species of this genus.

#### *Stages in the Life History*

Three collections No. 5769, 5770, and 5771 of the United States National Museum contain immature forms of this species. Collection No. 5771 contains both immature and sexually mature worms. The very young stages found in the two collections from the muskrat agree so well with the immature forms from *Aix sponsa* that it is impossible to differentiate the two forms and consequently they are taken to be identical.

The most immature specimens have apparently just burst out of the cysts since the pigmentation can be seen quite as perfectly as in most Notocotyloid oercariae. The pigmentation in this species agrees generally with that described by Cort (1914) for *Cercaria urbanensis*. The pigmentation remaining is arranged around the lateral eye spots (Fig. 19) and the lateral pigmented lines extending from the eye spots to near the posterior end. Aside from this there is a very diffuse pigmentation throughout the entire body. From the time of encystment of the cercaria to the youngest stages at hand considerable change has taken place. The anterior eye spot has been lost and the general pigmentation as described above is generally much reduced as compared with the heavily pigmented *Cercaria urbanensis*. The locomotor pockets have been resorbed so that no trace of them exists in the youngest stages at hand. Development of the ventral glands is the most conspicuous change which has taken place. Figure 14 shows diagrammatically the youngest stage studied in which three ridges or keels are thrown out on the ventral side. The median one being about twice as high as the lateral ones which are ventral in position to the intestinal crura (Fig. 12). Along the median ridge the papillae altho only partially differentiated are clearly seen. The lateral ridges show indistinct irregularities which in section are clearly the beginnings of the papillae. No trace of the outer rows of papillae which occur in *Notocotylus quinqueserialis* have been observed. In more mature stages the ventral papillae are distinctly seen (Figs. 17, 19).

Faust (1918) stated that in the Monostomata the paired ceca are filled with a jell and are nonfunctional in the cercaria stage. In contrast to this the ceca in the youngest stages studied, which are of course well past the cercaria stages Faust studied, show that changes have taken place in this feature. The ceca in these stages show the intestine as a tube (Fig. 12) whose walls are surrounded by large nucleated cells. Totos in this stage of development also show distinct but small internal and external diverticula (Fig. 19).



The genital glands show little development over that of the cercariae. The ovary and testes are made out readily in the toto mount as well as the cords of cells which are to differentiate into uterus, vagina, vas deferens and cirrus. In more mature stages differentiation of the cirrus and vagina is well started so that the relative length of the two organs can be determined.

In the more mature specimens represented in figure 17 the genital glands have made a tremendous growth and appear very much as in the sexually active worm. The uterus, however, is less distinct and probably still non-functional. It is in this stage that the vitelline glands make their first appearance and here appear as single celled isolated follicles. The ducts of these follicles cannot be traced so that it is impossible to determine if the relation found by Faust (1918), namely that the vitellaria of Notocotyliids are composed of five inner and three outer portions, obtains in this species.

Of the seven larval Monostomata described from North America, viz.  
*Cercaria hyalocauda* Haldemann 1842    *Cercaria konadensis* Faust 1918  
*Glenocercaria lucania* Leidy 1877    *Cercaria aurita* Faust 1918  
*Cercaria urbanensis* Cort 1914    *Cercaria robusta* Faust 1918  
*Cercaria pellucida* Faust 1918

the immature stages described above resemble more closely *Cercaria urbanensis* Cort (1914) than any other known monostome cercaria. Based on the similarity of the excretory system, of the genital organs, on the pigmentation and on the late differentiation of the vitellaria, no trace of which has yet been found in *Cercaria urbanensis*, it seems highly probable that these forms can be actually connected. Hence while demonstration of the life history by experimental methods has not at this time been given, it seems justifiable to accept *Cercaria urbanensis* as the larval form of this Notocotyliid.

#### NOTOCOTYLUS QUINQUESERIALIS (Barker and Laughlin)

Syn: *Monostoma* sp. Stiles and Hassall 1894

*Notocotyle quinqueseriale* Barker and Laughlin 1911

Medium sized to large Notocotyliids with wedge shaped body 2.5 to 4 mm long by 0.66 to 1.33 mm in maximum width which is found at the level of the ovary. Anterior end more or less pointed, posterior end rounded. Dorsal surface smooth, convex, ventral concave, unarmed but possessing five longitudinal rows of adhesive glands or papillae. Each row containing from 16 to 18 distinct wart-like projections. Mouth sub-terminal, spherical 200 to 450  $\mu$  in diameter; esophagus short without pharynx. Intestinal crura irregular in shape and size with short internal and external diverticula. Genital pore between mouth and intestinal bifurca-



tion. Cirrus pouch extending from this point into the beginning of the second body third, being approximately one-third the length of the entire body. Vagina two-thirds the length of the cirrus pouch. The much lobed testes are situated in the posterior end, external to the intestinal crura. Ovary irregularly lobed, on a level with and between the testes, intracecal in position. Vitellaria extracecal, anterior to the testes, extending to the middle of the body.

Habitat: Intestine

Locality: Maryland

Date: 1892

Habitat: Intestine

Locality: Baker Lake, Washington

Date: August 13, 1915

Host: *Arvicola riparius*

Collector: A. Hassall

No. 5773 U.S.N.M.

Host: *Fiber zibethicus*

Collector: H. E. Metcalf

No. 15.120 Ward collection

The description of Barker and Laughlin while adequate states that the intestinal ceca are simple. A careful examination of the material at hand shows small, short diverticula both externally and internally throughout the length of the ceca. The writer has not had opportunity to study the material described by Barker and Laughlin.

#### CATATROPIS Odhner 1905

Body elongate, anterior and posterior ends usually equally rounded. Anterior half of ventral surface covered with three rows of non-protrusible papillae; median row set on a ridge or keel; lateral rows each containing 8 to 12 glands. Vagina strongly developed, usually as long as the cirrus pouch.

This genus was created by Odhner to hold *Catatropis verrucosa* (Frölich) which Odhner found to differ from *Notocotylus* in the character of the ventral glands, those of *Notocotylus* being protrusible while those found in *Catatropis verrucosa* were very much reduced, being in the form of a median ridge or keel in the median row and small embedded papillae or glands in the outer rows. It is similar to *Notocotylus* in its inner organization and differs from that genus in the fact that the ventral glands are not protrusible.

#### CATATROPIS FILAMENTIS Barker 1915

Syn: *Catatropis fimbriata* Barker 1915

Thin flat worms, gradually tapering anteriorly, 2.2 to 3.3 mm long by 0.56 to 0.7 mm wide at the level of the testes. Anterior half of the body covered with needle like spines arranged in oblique rows. Three rows of flattened papillae on the ventral surface, 12 to 13 in each row. Oral sucker spherical, 66 to 99 $\mu$  in diameter. Esophagus 105 to 132 $\mu$  in length. Pharynx wanting. Intestinal crura undulating. Testes two to four lobed, external to the intestinal crura. Ovary globular or oval 132 $\mu$  long by 105

to  $112\mu$  wide, margin irregular. Shell gland ovoid, anterior to and a little larger than the ovary. Cirrus pouch tubular, elongate, extending to the beginning of the second body third. Prostate gland and cirrus covered with papillae. Vagina straight, muscular, as long as the cirrus pouch. Vitellaria external to the ceca, extending from the middle of the body caudad to the testes. Excretory bladder forked, opening to the exterior just dorsal to the posterior end. Eggs thick shelled, 20 to  $22\mu$  long by  $11\mu$  wide, having two long polar filaments, one at each end.

Habitat: Duodenum

Host: *Fiber zibethicus*

Locality: Nebraska

Collector: ?

#### PARAMONOSTOMUM Lühe 1910

This genus, created by Lühe to hold *Monostomum alveatum* (Mehlis) Creplin, is characterized by Lühe as follows: Body compressed, egg shaped, greatest breadth a little caudad from middle of body, posterior end broadly anterior tapering and pointed; anterior half of ventral surface thick set with short heavy spines. Ventral glands absent. Cirrus pouch weakly muscular. Vagina usually one-half length of cirrus pouch.

Type species: *Paramonostomum alveatum* (Mehlis) Crepl.

American representative: *Paramonostomum echinum* nov. spec.

Barker (1916) criticises the erection of a new genus on the basis of the absence of the ventral glands on the ground that the number of rows vary from two in *Notocotylus diserialis* Ssinitzin to five in *Notocotylus quinqueserialis* Barker and Laughlin. Yet the same author accepts the genus *Catatropis* of Odhner founded on the non-protrusible character of these same glands. There is apparently as much reason to accept the genus of Lühe based on their absence as that of Odhner founded on their non-protrusibility.

#### PARAMONOSTOMUM ECHINUM nov. spec.

Thin cup-shaped worms, 2 to 2.5 mm in length by 0.6 to 0.7 mm in maximum width which is found at the beginning of the posterior third of the body length. No ventral papillae have been found on these worms, the anterior half of the ventral surface being covered with heavy spines  $5\mu$  in length. These curve caudad and are thick set according to the definite pattern shown in figures 13 and 16. Mouth terminal, spherical, 102 to  $125\mu$  in diameter, followed by a short esophagus which bifurcates to form the intestinal crura; these follow an undulating course to the posterior end of the body where they end blindly. Crura provided with short but definite internal and external diverticula. Genital pore situated just posterior to the intestinal bifurcation. Cirrus pouch extends from this point into the beginning of the second third of the body. Vagina one-half as long as the cirrus pouch. Prostate gland and cirrus without papillae.

Testes four lobed, extracecal, lying at the same level in the posterior end of the body. Ovary between the testes and separated from them by the intestinal crura. The three to four lobed ovary is usually elongated antero-posteriorly. The uterus as in other members of this genus is coiled transversely between the crura and extends from the level of the ovarian complex to the posterior end of the cirrus pouch at the beginning of the second body third. The vitelline glands occupy an extracecal position and extend from the testes to the middle region of the uterine coils which is found in the caudal portion of the second body third. Eggs numerous, medium thick shelled,  $20\mu$  in length and approximately twice as long as wide. They possess a long polar filament at each end.

Habitat: Intestine

Host: *Fiber zibethicus*

Locality: Wray, Colorado

Collector: C. H. Gable

Date: October 30, 1916

No. 21.91 Ward collection

#### NUDOCOTYLINAE Barker 1919

Small cup shaped Notocotyliidae with thick bodies, without ventral glands. Genital pores separate, ventral, lateral, in posterior half of body. Cirrus pouch pear-shaped, enclosing small portion of seminal vesicle. Vitelline glands strongly developed compact masses, lateral to ceca and anterior to testes. Uterus in transverse folds, in anterior half of body, extending laterally over intestinal crura.

Type genus: *Nudocotyle* Barker 1916

Barker would include *Barisomum* Linton 1910 in this sub-family. This is a doubtful decision since in the genus *Barisomum* the genital pore is in the anterior body third and the shell gland lies posterior to the ovary. It possesses in fact certain Notocotyloid characters but conforms more closely to the Pronocephalidae than to the Notocotyliidae in the position of the genital pore, and the character and position of the genital glands.

#### NUDOCOTYLE NOVICIA Barker 1916

Small thick oval worms, 709 to  $899\mu$  in length; 500 to  $657\mu$  in breadth. Anterior end tapering gradually, posterior markedly truncate. Dorsal surface strongly convex, ventral concave. Body smooth, devoid of ventral papillae or spines. Oral sucker subterminal, spherical 50 to  $65\mu$  in diameter; pharynx wanting; intestinal ceca undulating but without diverticula. Male and female genital pores separate, ventral, lateral, in beginning of posterior body third. Cirrus pouch large, club-shaped, about one-third of body width in length. It lies transversely and median in anterior portion of posterior body half. Cirrus without spines. Testes extracecal in position, lying in same level in posterior fifth of body, frequently 2 to 5 lobed. Ovary elongated, convoluted or lobed, in extreme posterior end of body between testes and separated from them by intestinal crura. Shell gland



compact, anterior to ovary. Laurer's canal and receptaculum seminis were not observed by Barker. Eggs oval, twice as long as wide, 20 to 24 $\mu$  long 10 to 13 $\mu$  wide. With long polar filament on each end about five times as long as egg itself.

#### HERONIMIDAE Ward 1917

This family was created by Ward (1917) to hold the two aberrant genera *Heronimus* MacCallum (1902) and *Aorchis* Barker and Parsons (1914). Ward called attention to the close resemblance of the two forms and suggested that they might prove to be identical. He characterized the family as follows: "Moderate sized monostomes with thick, elongate, soft body, slightly flattened, tapering toward both ends. Oral sucker weak; pharynx large; esophagus short or absent; ceca simple, narrow, extending to posterior tip but not united. Vitellaria compact, tubular. Uterus with four longitudinal regions; genital pore ventral to oral sucker, near anterior tip. Testis tubular, small; copulatory apparatus poorly developed. In lungs of turtles, northern North America."

One year later (1918) the same author restated the family diagnosis with the following addition: "Vitellaria compact tubular, shaped like an inverted V. Testes tubular, lobed or with short branches, united into a V-shaped organ with the apex anterior," and again stated that the two forms probably belonged to the same genus. About a year later Stunkard (1919) presented a paper in which he showed that the apparent difference in the two forms was due largely to the partially diagrammatic figure of MacCallum (1902) and to the discrepancies in the description of Barker and Parsons (1914) and that the two forms are identical, thus not only belonging to the same genus as suggested by Ward but representing a single species, *Heronimus chelydrae* MacCallum.

#### HERONIMUS CHELYDRAE W. G. MacCallum 1902

Syn: *Aorchis extensus* Barker and Parsons 1914

*Aorchis extensus* Ward 1917

*Monostoma* sp. Stiles and Hassall 1894

The genus was created by MacCallum (1902) to include worms collected from the lungs and bronchi of *Chelydra serpentina*. The genus stands according to MacCallum "in many respects far apart from the other genera," especially in the position and nature of the genital opening, in the complicated structure and course of the uterine tract, in the unusual formation of the yolk glands, in the presence of but one testicle and in the position of the excretory pore. The genus may be recognized by the following diagnosis: Medium to large monostomes with semicyclidrical body tapering slightly towards both ends; strongly muscular. Mouth



opening terminal, oral sucker small, pharynx weak but distinct. Esophagus very short; intestinal ceca simple, ending blindly in the extreme posterior of the body. Genital pore inconspicuous, median, ventral to the pharynx. Ovary situated in the anterior one-fourth of the body, lateral, usually intracecal; shell gland smaller than the ovary and posterior to that organ. Receptaculum seminis present, usually about two-thirds as large as the ovary. Laurer's canal absent. Uterus, except for the four longitudinal loops, coiled around the intestinal crura from the level of the ovary to the posterior end of the animal. Vitelline gland a coarse, compact U-shaped, closed tubular structure, dorsal to the intestine. Testis U-shaped, closed portion cephalad, about one-fourth the body length from the anterior end. The tubular, irregularly lobed testicular mass extends caudad to a level about one-eighth the body length from the posterior end. Protrusible, non-muscular cirrus present. Excretory pore median, anterior, dorsal to the pharynx. Eggs large, ovoid, thin shelled, containing fully developed miracidia in the metratrum.

The anatomy of this form is well described by MacCallum (1902) and Barker and Parsons (1914, 1917), and with the additions and corrections of Stunkard (1919) calls for no further anatomical discussion here.

The writer has been given an opportunity to examine the type specimen of this species deposited in the United States National Museum and can verify the statements of Stunkard on the specific identity of the two species.

MacCallum reported the original material from *Chelydra serpentina* taken in the Grand river at Dunville, Ontario, Canada. Barker and Parsons (1914) report from *Chrysemys marginata* taken in Lake Emily, Minnesota, and the Mississippi river and later (1917) in the same host taken in the Mississippi river near Fairport, Iowa. At this time they call attention to the distribution in Illinois.

Ward (1917) reports this species from "various turtles" taken in Michigan, Indiana, Illinois and Nebraska. Stunkard (1919) collected this species from *Chelydra serpentina* taken in Illinois, Ohio, North Carolina and Texas; in *Chrysemys marginata* taken in Iowa, Illinois, Missouri and Kentucky; in *Pseudemys elegans* and *Malacoclemmys geographicus* in Illinois; *Aromochelys odoratus* and *Kinosternum pennsylvanicum* in North Carolina. The specimen listed by Stiles and Hassall (1894:253) as "*Monostoma* sp.—*Chelonia* gen. sp. (bronchi)—Illinois-Forbes-Leidy" belongs here.

The writer has found this species in *Chelydra serpentina* and *Chrysemys marginata* taken in the drainage ditch at Urbana, Illinois; in *Chrysemys marginata* taken in the Mississippi river near Fairport, Iowa; in *Graptemys geographicus* taken near Chicago, Illinois; in *Chelydra serpentina* and *Chrysemys marginata* taken in Minnesota and in *Kinosternum pennsylvanicum*, *Kinosternon odoratus*, and *Chrysemys picta*, a new host, taken in North Carolina.

While this species was reported by MacCallum as "not by any means a constant parasite," he having found it in only one host infected of a number examined, more recent data show this worm to be rather constantly present. In seven specimens of *Chrysemys marginata* collected in the summer of 1911 from Lake Emily, Minn., Barker and Parsons found five infected, one of them yielding thirteen worms from both lungs. The same authors (1917) found that female turtles were more than three times as heavily infected as males, Stunkard (1919) from the examination of "about three hundred turtles" reports the heaviest infection in one host as six. On an examination of "more than fifty turtles" he found no difference in the relative infections of males and females. The writer has examined one hundred and two hosts of six different species and of these forty-four showed infection with these worms. The highest percentage of infection for any species was found in *Cinosternum pennsylvanicum* from North Carolina in which 34 out of 45 specimens or approximately 75 percent were infected. The highest number of individuals from a single host of this species was eleven while a single individual of *Graptemys geographicus*, and the only one of eighteen which showed infection, carried twelve worms in both lungs.

During the past four years the writer has had opportunity to examine more than one-hundred turtles as stated above. It was noted early in the investigation that the collections made in different seasons showed no striking difference in percentage of infection. It was then undertaken to determine if possible the length of life of this parasite in the definite host. It is generally understood that most intestinal parasites have an annual cycle and depend on this for continuity of the species. However, data on this point seems lacking in this group. The work on *Heronimus chelydrae* consisted in the examination of a number of turtles collected in the same region, Raleigh, North Carolina, at various seasons of the year.

Some of these dissected on arrival showed relatively heavy infections, others which were kept in the laboratory aquaria for periods of six, twelve and eighteen months still carried infection, and a single specimen of *Chelydra serpentina* which had been kept in an aquarium for more than three years yielded two specimens of *Heronimus chelydrae* and a single nematode, probably *Camallanus americanus*. As was stated above hosts examined when taken, usually carry intestinal forms in addition to the lung fluke already mentioned, while those which have been kept in aquaria for a period of six months or more show a marked reduction in the number of the intestinal forms. There is no apparent change in the number of the lung flukes present.

Little is known regarding the condition of parasites during hibernation of the host. Blanchard (1903) records that hibernating marmots do not contain any intestinal parasites. Ward (1909) reports observations carried out on the frog, *Rana virescens*. In this he says that parasitic infection increases steadily up to hibernation, and does not decrease during the latter

period; that the parasites reach the climax of sexual maturity soon after the host emerges from the winter quarters. They discharge their eggs and pass out from the body of the host soon after the time of spawning, and at the close of this period the hosts are relatively free from infection.

Observations of the writer verify the sexual inactivity of the parasite *Heronimus chelydrae* during the early part of the winter and the copious discharge of mature miracidia in early spring. On the other hand these turtles did not become free from infection at any time during the period of the experiment. It must be kept in mind however that the turtles used were not subject to natural conditions, i.e., no opportunity was afforded for hibernation and no eggs were deposited during this time. That trematodes adapted to partially closed cavities can live longer than for a single reproductive phase is evident, since in the instance reported above in which the host has been kept for a period of more than three years, the two parasites found were sexually mature, and were producing large quantities of ripe eggs when the host was examined; this is true also in one other case in which the host was kept for more than eighteen months.

#### COLLYRICLIDAE Ward 1917

This family was created to hold the genus *Collyriclum* of Kossack and is circumscribed by Ward as follows:

"Small to moderate sized monostomes with discoidal compressed, not muscular body, broader than long. Oral sucker weak; pharynx present; ceca simple, long, capacious, not united. Genital pore ventral near center of body. Vitellaria follicular, scanty, antero-lateral; ovary much lobed, symmetrical. Uterus posterior, in irregular coils which show an antero-posterior tendency, terminal region enlarged. Testes oval, symmetrical, behind ovary. Eggs very small. Adults parasitic in dermal cysts on abdominal surface of the skin of birds."

In the light of our present knowledge of these forms the family diagnosis must be modified with respect to the condition of the testes. Tyzzer (1918) has shown the testes of the American species to be irregularly lobed and not oval as described for the European species, *Collyriclum faba* by both Kossack (1911) and Jegen (1917). The writer has examined a number of specimens of *Collyriclum colei* Ward and has found the observation of Tyzzer stated above to be correct.

Type and only genus: *Collyriclum* Kossack 1911.

American representative: *Collyriclum colei* Ward 1917

#### COLLYRICLUM COLEI Ward 1917

Syn: *Monostoma faba* Cole 1911

*Collyriclum faba* Tyzzer 1918

*Diagnosis:* Small hemispherical worms, 4 to 5 mm in length and breadth by 3 mm thick. Cuticula covered with spines  $35\mu$  in length, arranged in groups which form rather regular rows around the worm. Mouth terminal



or slightly dorsally placed, surrounded by a muscular sucker  $220\mu$  long by  $375\mu$  wide. Pharynx smaller  $140\mu$  long by  $125\mu$  wide, adjacent to the sucker, followed by short esophagus which bifurcates to form the large voluminous simple intestinal crura; these end blindly at the end of the middle body third. Genital orifice ventral, near center of body. Testes near the ends of the crura, lobed, the main portion pear-shaped. Ovary in intestinal bifurcation, three branched, each division containing from 5 to 10 lobes. Vitellaria well developed, imperfectly symmetrical with 5 to 7 groups on the left and 7 to 9 on the right. Uterus much coiled, generally in the posterior half showing a tendency to antero-posterior coiling. Eggs small, 19 to  $22\mu$  long by 10 to  $12\mu$  wide, containing in the end portion of the uterus a fully formed miracidium.

The anatomy of these worms has been so thoroughly discussed by Tyzzer (1918) for the American species, and by Kossack (1911) and Jegen (1917) for the European species that it does not seem necessary to enter into a detailed discussion here. I desire instead to give a comparison of the two forms since Tyzzer found reason based largely on the inconsistency of Kossack's description and figures to declare the American material identical with that found in Europe.

Ward (1917) after examination of the material reported by Cole (1911) as *Monostoma faba* pointed out distinct differences between this and the European form described by Kossack (1911). The following is his statement, "As a cause of an epidemic among sparrows at Madison Wisconsin, Cole (1911) reported under the name of *Monostoma faba* a trematode that in reality differs distinctly from the European species. The form of the ovary, the extent of the vitellaria, the dermal spines, and other details of structure disagree with the recent description of Kossack who, moreover, assigned Rudolphi's species." [erroneously attributed to Rudolphi, really Bremser (1831)] "to his new genus *Collyriclum*. The American form constitutes a new species in this genus and to it the name *Collyriclum colei* may be given."

One year later (1918) the same author restated the differences in the two species as follows: "These specimens differ clearly from the European form in numerous minor details, such as ovary, yolk glands, dermal spines, etc., and demand recognition as a distinct species under the name given here."

Tyzzer (1918) made a comparison of the two forms based on Kossack's description of *Collyriclum faba* and concluded that the two species were identical despite certain distinct differences which he explained away on the basis of the discrepancies between Kossack's description and figures. The work of Jegen (1917) which reached America after Tyzzer's had appeared verifies in a large measure the description of Kossack and leaves little doubt that the American material is distinct from *Collyriclum faba*. The following is the diagnosis of this species as given by Jegen: "In Cysten



Table I. Comparison of *Collyriclum faba* with *C. colei*  
After Tyzzer, 1918, with additions from Jegen, 1917

	European Material <i>Collyriclum faba</i>	American Material <i>Collyriclum colei</i>
Shape	Somewhat hemispherical.	The same. Minor additional points noted.
Size	4.2–4.8×4.5–5.46 mm Jegen from <i>P. domesticus</i> 4.4–5.2×6–5.4.	4.1×4.8×2.9 mm.
Mouth	Ventrally placed.	Dorsal to margin of body. In flattened specimens appears ventral from over-riding of larger dorsal surface.
Uterus	Similarly arranged in both.	
Intestine	Identical in form.	and extent.
Vitellaria	Symmetrical, each with seven rarely six or eight, follicle groups.	Not perfectly symmetrical, five to seven on left and seven to nine follicle groups on right side.
Ovary	T-shaped, each of three divisions with four or five branches. Jegen reports 5–7 lobes.	Of similar form, each division from 5–10 lobes.
Testes	Oblong or saber-shaped.	Showing three or more large processes and other minor irregularities, and curved over the blind ends of the intestine. In gross specimens seen only in part, appearing oblong or saber shaped. Measurement not feasible.
Genital orifices	General agreement in both.	
Oral sucker	0.204,5 to .441, 2 mm. Jegen, 0.3 to 0.45 mm.	Average, 0.219,8×0.375,3 mm.
Pharynx	0.129,1 to 0.193,7 mm. Jegen, 0.113 to .145 mm.	Average 0.140×.124,5 mm.
Spines	“Arranged in lines, with the individual spines apparently widely separated from one another.” Up to 35μ in length.  Jegen: in groups of 4 to 8, 28 to 35μ.	Set in annular rugae; maximum distance separating latter, .45 to 53μ. Up to 35,5μ in length. Average dorsal, 27,9μ long.
Ova	19,8×9,7μ.	19 to 21,4×10,6–11,6μ. Average 20,5×11,3μ.

zu zweien vorkommende Trematoden. Körperform annähernd rund. Dorsale Fläche stark gewölbt, ventrale weniger gewölbt bis flach. Haut mit Stacheln besetzt, die in Gruppen von vier bis acht Einzelstacheln stehen. Mundsaugnapf endständig. Darmschenkel einfach und zwei Drittel der Breite des Körpers einnehmend. Bauchsaugnapf fehlt. Terminal am Hinterende eine muskelreiche Partie, die bei der Fortbewegung als Saugorgan wirkt. Genital pori auf einer papillenartigen Erhöhung, median etwas vor der Körpermitte gelegen. Excretionsblase birnförmig und bedeutend über die Mitte hinausreichend. Dotterstöcke aus zwei seitlich gelegenen Follikelgruppen (7) bestehend. Hoden dorsal, den Darmschenkelspitzen genähert. Keimstock vor den Hoden, im ersten Körperdrittel, aus drei lobösen Gruppen bestehend. Schalendrüse unmittelbar neben und unter dem Keimstock. Laurersche Kanal vorhanden. Receptaculum seminis fehlt. Uterusschlingen hauptsächlich im hinteren Körperteil. Eier ohne Filamente, mit scharf abgesetztem Deckel und einer kleinen, seitlichen Spitze am entgegengesetzten Pol, sehr zahlreich."

Because of the distinct differences shown by Tyzzer his table is incorporated with Jegen's corrections to Kossack's description of *Collyriclum faba*. It is printed on preceding page of this paper.

A study of the table shows clearly that the species in question differ with respect to the asymmetry and extent of the vitellaria and the form of the testes. In regard to the agreement of the American material with Kossack's description Tyzzer says: "that the American material agrees very closely in most respects with Kossack's description, there being similarity of size and shape, in the appearance of the alimentary canal and uterus, and in the position of the genital orifices. The measurements of the oral sucker, pharynx, esophagus, spines, and ova correspond rather closely, and such differences as occur appear to be within the limits of species variation."

Regarding the grouping of the spines Kossack (1911:574) "Die Haut ist mit Stacheln bedeckt, die in regelmässigen Reihen angeordnet sind. Die einzelnen Stacheln sind ziemlich weit voneinander entfernt und durchschnittlich 0.035 mm lang." Jegen describes the spines as being arranged in groups in rows. Four to eight spines in a group, and says, "Kossack erwähnt (S. 574) dass die Stacheln in regelmässigen Reihen angeordnet seien. Ich glaube nun nicht, wie Odhner dies ausspricht, dass er die Stachelgruppen übersehen hätte, wenn sie überhaupt in seinem Material vorhanden waren. Vielmehr liegt die Möglichkeit vor, dass er ein Entwicklungsstadium vor sich hatte, bei dem die Gruppen noch nicht vollständig gebildet waren."

Tyzzer calls attention to the ovary which he says "presents more lobules than was noted by Kossack." Jegen states that the ovary is very strongly lobed and found: "An jedem der drei Aste sitzen fünf bis sieben

solcher einzelner Knollen." Tyzzer states further that "the basis for differentiation of an American species at the present time appears therefore to be rather inadequate." That he is dealing with the same species as that reported by Cole (1911) and later named *Collyriclum colei* by Ward (1917) cannot be doubted and according to his statement his material "is undoubtedly of the same species."

Although Tyzzer failed to find any difference which would warrant a second species of *Collyriclum* the present investigation has shown that except in minor detail the work of Jegen agrees with that of Kossack, and on the basis of the descriptions of these investigators the American material is distinct from *Collyriclum faba* in that the testes are lobed and in the asymmetry and extent of development of the vitellaria. It is impossible to explain away these differences either as "artefacts in preservation" or as "individual variation," nor is it probable that both Kossack and Jegen have overlooked these features. On the basis of these difference the American material must be recognized as a distinct species under the name *Collyriclum colei* Ward.

A preliminary study of specimens of *Collyriclum faba* secured by Professor Ward bears out the description of Kossack and Jegen as well as the conclusions of the writer drawn from the study of their papers and comparison with American specimens of this genus. A more thorough study of the European material is not feasible at this time but is anticipated at an early opportunity.

#### REMARKS ON THE LIFE HISTORY

The life history of *Collyriclum faba* is doubtfully known. Tyzzer gives a careful description of the development of the egg of *Collyriclum colei* from the time of fertilization to maturity in the end portion of the uterus. Regarding the mature eggs he says "The eggs stored in the terminal portion of the uterus evidently contain miracidia, the morphological features of which are not clear in fixed material owing to imperfect preservation and shrinkage." He continues with a description of the "hair-like" structures which have been distinguished. This adds evidence that a miracidium is present.

The work of Jegen (1917) which is an attempt at the life history of *Collyriclum faba* differs radically from the statements of Tyzzer in that he finds the eggs contain two embryos which are not miracidia but young trematodes; these need only to be incubated in the intestine of the host that they may break out of the egg shell and freed with the excrement, may wander into the feather follicle. He found also cysts (Dauercyste) which after a longer period of incubation break open and the worm enters the follicle of a feather. Jegen summarizes his work as follows: "Die Eier von *Collyriclum faba* werden durch den Wirt mit dem Parasiten aufge-



pickt und gelangen in den Vogeldarm, wo die Embryonem ausschlüpfen. Mit den Excrementen werden letztere ins Freie befördert, wo sie, sofern die Möglichkeit zur Infektion vorhanden ist, direkt in die Federfollikel der jungen Vögel einwandern. Im andern Fall bilden sich Dauercysten, die nach längerer Entwicklungsruhe sich auflösen und den eingeschlossenen Organismus frei lassen, so dass er ebenfalls in die Federfollikel einwandern kann." This summary of Jegen is supported by experimental evidence gained by incubation of the eggs in a portion of the intestine of an infected bird as well as by numerous attempts to incubate the eggs which had not passed through the intestine of the host altho he says these gave negative results. The "Dauercysten" he found in excrement of infected birds, which was dried by exposure to air, and at other times in the nest and on the feathers of young sparrows.

The outline of Jegen gives essentially a direct development which omits the parthenogenetic stages observed in all cases where the life history of digenetic trematodes is known. Observations of the writer support the view of Tyzzer that a miracidium is present in the mature egg in the uterine egg sac. The fully developed miracidium shows well developed germ balls. This is in direct contrast to the findings of Jegen who says that the embryo contains two well developed germ balls with numerous others which disappear later in course of development. Jegen found that the eggs would develop only in the intestine of the host and when fed to uninfected birds empty egg shells and embryos were found on the second and third day. He neither states nor demonstrates that these experimental birds became infected with the adult parasites.

The work of Jegen dealing with the life history of *Collyriclum* is full of gaps. The life history as given is bridged over by supposition. The infection of the sparrows by feeding of eggs is not demonstrated, only the presence of embryos which may well be miracidia. Jegen does not demonstrate beyond doubt that these cause the formation of the cysts in the sparrow. The "Dauercysten" which he says infect directly the host based on his experiment of the dried excrement certainly serve to protect the parasite from dessication until it can reach the intermediate host; nothing indicates whether this be a miracidium or another infective stage; and the periodicity of occurrence of the adult parasite in correlation with a rainy season tends to show that the former is the correct interpretation.

The work of Jegen is apparently a misinterpretation of the life history and leaves much to be done in order to demonstrate the facts. The only clear contribution of this author to the life history of this form lies in the discovery of the "Dauercysten" which he apparently misinterpreted. Many more extensive and careful experiments must be carried out in order to demonstrate conclusively the complete life history of this form.



## Species Inquirendae

## CLINOSTOMUM (?) INCOMMODUM (Leidy)

Syn: *Monostomum incommodum* Leidy 1856*Distoma oricola* Leidy 1884*Distomum incommodum* Leidy 1890*Monostomum incommodum* Leidy 1904

*Monostomum incommodum* is described by Leidy as follows: "Body compressed, above convex, below concave, sides parallel anteriorly convex, posteriorly angularly convex. Head continuous with the body, obliquely truncated. Mouth round, surrounded with a wide circular lip which is emarginate below. Male generative aperture? communicating with a hemispherical cavity (acetabulum?) one-fourth the length of the body from the head. Length 9 lines, breadth  $1\frac{1}{2}$  lines.

Habitat: Fauces

Host: *Alligator mississippiensis*

Locality: Florida

Collector: J. W. Bailey

Date: Previous to 1856

Leidy (1890) places this species as *Distomum incommodum* and as a synonym of this species his *Distoma oricola* from the mouth of *Alligator mississippiensis*. On the basis of the later determination of Leidy (1890) his description of *Distoma oricola* is here included for the purpose of comparison and as evidence for the disposition of *Monostomum incommodum*.

*Distoma oricola* Leidy 1884

"Body elongated elliptical, moderately wider and thicker posteriorly and ending in a blunt, angular extremity, convex dorsally and flat ventrally, unarmed, smooth or minutely wrinkled transversely. Mouth subterminal, and enclosed with a reniform lip succeeded by a linear annulus. Acetabulum large, globular, included at the anterior fourth of the body, and opening ventrally by a conspicuous central aperture. Generative orifice ventral, at the posterior fourth of the body. Length, 15 to 20 mm; breadth, 3 mm. Eight specimens obtained from the mouth of the alligator, *A. mississippiensis*, in Florida, by Mr. Stuart Wood."

Pratt (1902) surmises that this species is allied to the genus *Clinostomum*. This view is supported by Ward (1918). Then if, according to this view the determination of Leidy, that *Distoma oricola* is a synonym of *Monostomum incommodum* which he determined later (1890) as a *Distome*, *Distomum incommodum*, be accepted, *Monostomum incommodum* is likewise allied to the genus *Clinostomum*.

## MONOSTOMUM ORNATUM Leidy 1856

Syn.—*Monostomum ornatum* Brandes 1892*Monostomum ornatum* Braun 1893*Monostomum ornatum* Diesing 1858*Monostomum ornatum* Monticelli 1892*Monostomum ornatum* Stafford 1902

This species was described by Leidy as follows:

"Body slightly compressed ovoidal, anteriorly broad; yellow variegated with brownish red. Mouth infero-terminal, acetabuliform, transversely oval. Penis conical, protruding a short distance below the mouth. Female aperture a short distance below the penis. Length 1 to  $1\frac{1}{2}$  lines, breadth  $\frac{1}{2}$  to  $\frac{3}{4}$  line, thickness  $\frac{1}{4}$  to  $\frac{1}{2}$  line."

Habitat: Body cavity

Host: *Rana pipiens*

Locality: Philadelphia

Collector: H. W. Warren

Stafford (1902) questions the determination of these worms and conjectures that they belong either to the genus *Haematoloechus* sp. which is commonly found in the lungs of frogs or to *Dist. quietum* or *Cephalogoni-mue amer.* and have been liberated in the first case from the lung and in the other cases from the small intestine of the host. He inclines to the former view "on account of the ease with which the small ventral sucker may be overlooked and the readiness with which worms may be freed from the lungs without observation." He adds that, "it is unlikely to be *Distomum quietum* from the position of the genital openings" and that "it could scarcely have been *Dist. retusum* (*Ceph. amer.*?) since he reports it also in the same paper although he does not describe it there but in an earlier number."

In regard to the habitat of *Monostomum ornatum* Stafford says that "of the hundreds of frogs I have examined I have never yet found a Trematode free in the body cavity and I doubt if anybody else has ever obtained one that did not first get there by the accidental cutting or tearing of some other organ."

The above assumption of Stafford that trematodes do not occur free in the body cavity of frogs appears to be doubtfully correct. Osborn (1922) and Cort (1913) report encysted *Clinostomum* in the body cavity. The writer in examination of numbers of frogs has been able to observe these and has several times found some of these worms out of their cysts and free in the body cavity. These frogs were opened most carefully and worms that might have been freed by the cutting of the body wall could not have found their way to remote parts of the cavity in the time consumed by the operation and examination. On the other hand it is hardly probable that the dozen specimens recorded should escape from the lungs unnoticed as suspected by Stafford and none be left to show the normal habitat. However, as Stafford has noted and as was stated above, the worm could scarcely have been *Distomum retusum* (*Cephalogonimus americanus*?)

since it is recorded in the same paper. Stafford, however, has failed to note that Leidy recorded also in this same paper *Distomum variegatum* from the lungs of *Rana pipiens* which he also describes in the same "earlier number" in which he describes *Distomum retusum*. Hence *Haematoloechus* is ruled out as well. From the habitat of these worms the writer suspects that it may possibly be a larval stage of a species of *Clinostomum*. The description is so meager that it is impossible to place it in any definite manner.

#### MONOSTOMUM SPATULATUM Leidy 1858

Syn: *Monostomum spathulatum* Diesing 1859

The following description given by Leidy includes the only available data. "Body flat, oblong ovate, narrowing anteriorly, obtuse posteriorly, color white, with brown tortuous lines indicating the course of the oviduct. Mouth acetabuliform, circular. Testes three, alternating on each side posteriorly with the oviduct. Ovaries on each side finely lobulated. Generative aperture small a short distance behind the mouth. Penis undistinguishable. Length 3-4 lines: breadth  $\frac{1}{2}$  line.

Habitat: Gall-bladder.

Host: Fish species unknown

Locality: Eastern U. S.

Collector: Jeffries Wyman

#### MONOSTOMUM AFFINE Leidy 1858

Syn: *Notocotyle(?)affine* Barker 1916

Leidy described this species as follows: "Body spatulate narrowest anteriorly, flat; posterior end obtuse, with an excretory orifice communicating with a well marked canal traceable as far forward as the commencement of the oviduct. Mouth round, oral acetabulum small, followed by a smaller pharyngeal bulb. Intestine simple, traceable on each side to the posterior end of the body. Testes four, posterior to the position of the distended oviducts. Ovaries finely lobulated, situated on each side external to the position of the intestine; oviduct transversely tortuous and distended with brown ova. Penis ensheathed, long, tortuous, echinate. Generative aperture small, acetabuliform. Ova oval and prolonged at one pole, or sub-pyriform. Length of body  $6\frac{1}{2}$  lines; breadth 1 line."

"Four specimens were obtained by Dr. J. N. Corse from the bile-ducts and gall-bladder of the muskrat (*Fiber zibethicus*). Closely allied to *M. hippocrepis* Diesing, but has no trace of the horse-shoe like collar to the head."

As is stated previously in this work the suggestion of Barker appears to be a misfit on the basis of the pharynx, the echinate penis and the undivided excretory canal which Leidy says is traceable as far forward as



the beginning of the oviduct. These characters are fundamental differences such as are used to separate families and groups and on the basis of these differences the supposition of Barker (1916) seems untenable.

MONOSTOMUM ASPERUM Vaillant 1863

Syn: *Monostomulum aspersum* Brandes 1892

*Monostomum aspersum* Pratt 1902

Vaillant described this species as follows: 1.4 to 1.9 mm long by 0.94 mm wide, elongated, both ends rounded; dorsal surface convex, ventral flat; cuticula in the anterior  $\frac{5}{6}$  densely covered with small spines regularly spaced and arranged in alternating rows. Mouth opening round. The digestive system composed of muscular esophageal bulb, followed by a long esophagus which extends to the middle of the body where it bifurcates to form the two ceca which extend to the level of the excretory bladder. The excretory bladder forms a semi-oval sac, which occupies the posterior end of the animal. The genital organs are between the excretory bladder and the ends of the intestinal ceca. The male organs are composed of a curved spinous penis, with a testicle, a vesicula seminalis and a deferent canal. The female organs are wanting or in some individuals incompletely developed and consist only of a granular cell mass.

Found in transparent sub-epidermal cysts of *Siren lacertina*.

In a later paper the same author (Vaillant, 1863a:347) expresses doubt in regard to his interpretation of the sex organs which he says appear to be only poorly developed.

On the basis of the descriptions of Vaillant, Brandes considered this as a larval form but attempted no further indication for the disposition of the species. Monticelli (1892) enumerates it without any attempt to determine its rightful place. Pratt assigns to it the same place as did Brandes.

Both accounts of this worm are such that the inference may be readily drawn regarding its larval nature. Neither account gives evidence of any individual in a sexually mature state. The sex organs are poorly developed and no mention is made of a uterus or of eggs which would indicate sexual maturity. The exceptional habitat assigned to this worm by Vaillant which he says is comparable to that of *Monostomum faba* Bremser is not so rare in the light of the present knowledge of the life histories of distomes and is quite in contrast to what is now known of the monostome life history. Many distomes are known to pass a portion of their life cycle encysted in the skin and superficial layers of the body, while no such stage has yet been found in the cycle of a monostome. The description of Vaillant as well as his figures are so inadequate that it would be hazardous to speculate on the systematic position of this form more than to say on the basis of the digestive system the cuticular spines and what has been given regarding the genital glands that it is probably the immature stage of a distome.



## MONOSTOMUM AMIURI Stafford 1900

This trematode taken from the swim bladder of *Amiurus nebulosus* by Stafford, is described by him as follows: "About 5 mm long and 2.25 mm broad much flattened and is broadest in its posterior two-thirds, the anterior third narrowing towards the mouth-sucker. The living animals are very soft bodied, inactive creatures."

"The integument bears a cuticle and is apparently very thin the sub-cuticular and glandular parts seem to have a similar structure to the same parts of the Distomes with which I am most acquainted. The intestinal system begins with the mouth whose thick muscular walls form the oral sucker. Following this is a muscular pharynx and a narrow esophagus which gives rise to two lateral intestinal ceca, extending as broad tubes to near the posterior end of the body where they end blindly."

"The posterior excretory bladder unpaired."

"The reproductive system is of the usual complex type. Each individual dioecious. The testes are situated most posterior in the body, between the median expulsion tube of the excretory system and the ends of the intestinal ceca, the vasa efferentia rise out of their anterior ends and proceed, by a direct course, to near the middle of the animal where they meet in the vesicula seminalis. This runs forward and opens by a muscular penis on the ventral surface of the worm, about one-third from its anterior end. The ovary is located a little behind the middle of the animal. The uterus filled with eggs occupies most of the posterior two-thirds of the body and opens by a bulbous vagina immediately behind and to the right of the penis. The two lobular yolk glands lie outside of the forked intestine and extend from the level of the genital openings to the hind end of the animal. A longitudinal yolk duct receives the yolk cells from the numerous follicles on each side and conducts them, by a transverse tube in the region of the ovary, to a yolk reservoir that communicates with the oviduct close by the shell gland. The egg is 45 by  $24\mu$  in size and its blunt broader end is provided with a short hooked filament."

The description and figure of Stafford shows a remarkable similarity to the Heterophyidae with which the worm agrees in having simple sac-like intestinal ceca extending to the posterior end, genital pore in immediate neighborhood of the ventral sucker if that organ is what has been interpreted as the female genital opening by Stafford. Testes oval, symmetrically arranged near the posterior end, seminal vesicle S-shaped, ovary oval, median, anterior to the testes. Vitellaria lateral to the intestinal ceca; extending from the level of the testes. The eggs also fall within the size found in this family but differ in having a short hooked filament at the blunt end. It differs also in that scales have not been recorded for this species by Stafford.

In the above comparison the bulbous vagina of Stafford has been construed to be the ventral sucker and considering this as a sucker this species agrees in every important anatomical feature with the Heterophyidae. The absence of scales here if they have not actually been overlooked could be considered only of specific import and according to the findings of Ward and Hirsh (1915:148) "spines and scales are caducous in life and are easily lost also if the specimens lie in preserving fluid for some time.

The fact that this species was found in the swim bladder of *Amiurus nebulosus* is not sufficient reason for its separation from the Heterophyidae since three genera of that family are known to have larval stages in fish, namely, *Metagonimus*, *Cryptocotyle*, and *Paracoenogonimus*. Ransom (1920:530) surmises that "Heterophyes," the genus to which *Monostomum amiuri* seems to be most closely related, "occur in their immature stages in fish," the adults thus far having been found in fish eating birds and mammals.

Habitat: Swim bladder

Host: *Amiurus nebulosus*

Locality: probably near Toronto,  
Canada

Collector: Stafford

## THE POLYPHYLETIC ORIGIN OF THE MONOSTOMES

From the earliest records of the Monostomata up to the present time this group of parasites has served for a dumping ground for inaccurately studied species in which the acetabulum has been wrongly interpreted or overlooked entirely. Many species have since been studied more carefully and consequently have been transferred to other genera. Out of this has arisen the problem of the origin of the Monostomata. Accumulative evidence has led to the belief that these forms are directly related to various other groups. This evidence is presented below.

Certain investigators of recent time have come to consider the trematodes of polyphyletic origin. According to Faust (1918) these conclusions are the result of "lack of study and consequent inability to recognize the fundamental resemblance of the genital, excretory and nervous systems."

The first to suggest relationship between the Monostomata and the Distomata was Monticelli (1893:149-150) when he called attention to the similarity of *Köllikeria* and *Didymozoon*. More recently Ariola (1906) reinforced this opinion by grouping *Monostoma fillicolle* Rud. and *Distoma okeni* Kölliker together on the basis of their anatomical similarity even though *Monostoma fillicolle* does not possess an acetabulum. MacCallum and MacCallum (1916) on the basis of anatomical similarity grouped together the two genera *Köllikeria* and *Nematobothrium* altho *Köllikeria* shows in many cases well developed acetabula while *Nematobothrium* is in that respect typically monostomatous.

Cohn (1904) in his study of *Monostomum flavum* Mehlis, worked over by Stossich (1902) and placed in the new genus *Typhlocoelum*, found a well developed but small ventral acetabulum which he figures in sagittal sections. This species on the one hand is apparently very closely related to the genus *Cyclocoelum* and was placed by Stossich in the same subfamily, *Cyclocoelinae*. On the other hand Cohn would transfer this to the *Fasciolidae* because of the presence of the ventral acetabulum which he says is diminished and in other instances often lost because of the shut-in habitat under which these worms live.

He adds as was stated previously the observation of a rudimentary mouth sucker in *Cyclocoelum mutabile* and in one other species of this group. Here he states that *Cyclocoelum mutabile* does not lack a primary sucker in many cases and like the Cestodarian *Amphilina* has lost hold-fast organs because of the lack of need for such organs in the cavities of the body of the host in which habitat these worms are wont to live. According

to this author *Cyclocoelum mutabile* and *Typhlocoelum flavum* are very closely related and because of different stimuli in their respective habitats, viz.: alveolar spaces, abdominal cavity and liver, occasionally the intestine for *Cyclocoelum*, and trachea and bronchi for *Typhlocoelum*, the acetabulum of *Cyclocoelum* has been lost while the oral sucker of *Typhlocoelum* has atrophied.

In his earlier work (1902) Cohn described *Monostomum oculobium* collected from *Vanellus melanogastrus* as having neither oral nor ventral suckers and relates it to *Cyclocoelum mutabile*. Fuhrmann (1904) describes a species, *Bothriogaster variolaris* collected from the intestine of *Rostrhamus sociabilis*, a South American Falconid, which from his figures and description appears to be very similar to *Monostomum oculobium* of Cohn. He states that in regard to the intestinal crura, absence of the oral sucker and the presence of only a pharynx it is like *Cyclocoelum mutabile*. The position of the genital glands is not the same but on the other hand is like those of *Monostomum oculobium* of Cohn. But it differs from *Monostomum oculobium* in that a ventral sucker is present which Fuhrmann believes Cohn had overlooked in his species. Fuhrmann would place *Bothriogaster variolaris* in the sub-family Syncoelinae of the Fasciolidae.

Odhner (1907) supports the view of Cohn and cites a number of instances to demonstrate it. Chief among these are, first, his genus *Aporocotyle* which is a blood parasite. He says that this suckerless form has its nearest relative in the distome *Haplotrema constrictum* (Leared), a blood parasite of the sea turtle. Second, those inhabiting the airsacs have developed the hold-fast organs to the least degree. This includes the Cyclocoelidae in which Odhner says all species are without a ventral sucker except for the recent discovery by Cohn of an entirely rudimentary acetabulum in *Typhlocoelum flavum*. He adds that in the Holostomes and Hemistomes ventral suckers have been greatly reduced and in some instances have disappeared entirely. In further support of this view he cites the reduction of the sucker in the male *Bilharzia* with the complete loss of this organ in *Bilharzia kovalewskyi*, and notes also the Echinostome like genus *Pegosomum* which inhabits the gall duct and has lost entirely the oral sucker. Odhner believes that the Monostomata will be finally split up and appended to other trematode groups, i.e., to the Distomes, Amphiostomes, Holostomes and perhaps others.

In the light of the foregoing one may well ask, what is a Monostome? The question has been aptly raised as to what characters or combinations of characters afford a reliable and accurate basis for the natural classification of the trematodes. On the basis of the examples given above the presence or absence of an acetabulum can be considered of relatively little importance and if such be the case other factors must be looked for in an attempt to establish a natural system of classification.



In view of the facts stated above the writer believes that an accurate knowledge of the more fundamental systems of organs will reveal group relationships which have heretofore passed unnoticed. In the present systematic groups homology of organs is a factor which has been generally passed over. This can best be demonstrated by a careful study of the developing organs in the early stages of the life history of the individual. Up to this time little has been done on the life histories of the Monostomata. Von Siebold (1835) and Van Beneden (1861) studied the early stages of the parthenogenetic phase. La Valette St. George (1855) described under the name of *Monostomum flavum* a cercaria which he believed to belong to this species. From his descriptions and figures one can see diagnostic points which tend to show that this cercaria belongs to the Notocotylidae on the basis of the well developed oral sucker, the possession of the locomoter pockets described by Looss, Cort, and Faust for Notocotylid species. The fact that La Valette St. George showed the intestine anastomosed posteriorly does not furnish evidence to the contrary since the crura of the Notocotylid approach each other in the posterior end of the worm and this may easily be mistaken for anastomosis or on the other hand the author may have misinterpreted the excretory ducts for the crura of the intestine. The characteristic features are the absence of the pharynx and the presence of the three eyespots which appear to be characteristic of the Notocotylidae. In addition to these Haldemann, Leidy, Cort and Faust have described some six or seven monostome cercaria from American hosts all of which have been referred to the Notocotylidae. While the writer has had opportunity to study immature stages of *Notocotylus urbanensis*, the preserved material has yielded only few facts that can be interpreted as of phylogenetic importance. These will be discussed in a subsequent section of this paper. As yet no Monostome life history has been demonstrated experimentally and the development of the important systems of organs has not been followed in the life history of even a single species. This seems to the writer to be a necessary step to be followed out in the major families in order to demonstrate the phylogenetic relationships of the large groups.

#### INTERRELATIONSHIP OF THE MONOSTOME FAMILIES

Before entering into the discussion of the probable origin of the Monostomes it seems fitting to discuss the interrelationship of the families as a unit or natural group of Trematodes. A comparison of the family diagnoses, given earlier in this paper, shows a striking contrast in each of the families discussed and of the families not included the same striking contrast may be drawn. No system of organs is the same in all of the families save perhaps the nervous system, so far as it has been made out, which is essentially the same in all the trematodes. The excretory system differs

in these families; in the Cyclocoelidae it is composed primarily of a large half-moon shaped bladder and ramifying network of anastomosed tubules. In the Notocotylidae a single club-shaped bladder extends almost to the ovary and sometimes a little posterior to the excretory pore (*Notocotylus quinqueserialis*); at the anterior end of this bladder two branches are given off which pass lateral to the ovary and from these numerous side branches are produced. In the Heronimidae the bladder consists of a large median sac with the pore in the anterior dorsal region, while in the Collyriclidae the bladder is single, club-shaped, and branches near the center of the body. In regard to the digestive system equally striking differences appear. The Notocotylidae show no trace of a pharynx while the Cyclocoelidae, Heronimidae and the Collyriclidae possess both sucker and pharynx. The crura of the Cyclocoelidae anastomose in the posterior end of the body while in the other families under consideration the crura end blindly. Another characteristic difference is the presence of dermal glands in some of the Notocotylidae, while such organs are unknown in the other families.

In the genital system are to be found equally great characteristic differences in the position of the glands with respect to the intestinal crura as well as in the form of the glands themselves. These and other important differences seem to indicate that these families have arisen from different lines.

#### THE APPARENT RELATION OF THESE FAMILIES TO OTHER GROUPS

Since the great diversity of structure in this group seems to indicate that the monostomes have arisen from different sources, there remains to be considered in conjunction with this fact the close affinity of certain of these families to widely separated groups.

The finding of a rudimentary acetabulum in *Monostomum flavum* Mehlis by Cohn and of the well developed acetabulum in *Bothriogaster variolaris* by Fuhrmann in the same year together with the similarity in structure seems to indicate a relationship to the Fasciolidae through the Syncoelinae according to Fuhrmann (1904) to which *Bothriogaster* is most closely related.

After a similar manner the Notocotylidae find their closest parallels among marine forms where the genus *Notocotylus* has anatomically a very close relative in *Adenogaster serialis* while those Notocotylids without the ventral glands appear more like the genus *Glyphicephalus*.

The Heronimidae stand alone in their organization and do not show close relationship to any known trematodes.

Attention was first called to the distome character of *Collyriclum faba* by Braun (1892) and again by Kossack (1911:577) who points out the relation of this species to *Distomum gastrophilum* but hesitates to decide whether it is a natural one, thus: "Indessen wage ich es vorläufig noch

nicht zu entscheiden, ob hier natürliche Verwandtschaft oder nur eine Konvergenzerscheinung vorliegt."

More recently Odhner (1914) placed this genus in his new family Troglotremidae which he characterizes as follows: Mehr oder weniger abgeplattete "Distomen" oder "Monostomen" von gedrungener Körperform und 2-13 mm Länge. Das äusserste Hinterende als ein kleiner "Schwanzanhang" vorstreckbar. Bauchfläche flach oder etwas ausgehöhlt, Rückenfläche gewölbt. Haut über und über mit spitzen Stacheln bewaffnet. Muskulatur bei den Cystenbewohnern schwach entwickelt, auch in den Saugnäpfen. Darmapparat mit Pharynx, nicht allzu langem Oesophagus and Darmschenkeln, die ein mehr oder weniger kurzes Stück vor dem Hinterende endigen. Exkretionsblase Y-förmig oder einfach schlauchförmig. Genitalporus dicht am Vorder- oder Hinterrand des ev. Bauchsaugnafes, median oder leicht lenkseitig. Cirrusbeutel meist fehlend, [except Troglotrema] Pars prostatica und Samenblase immer unterscheidbar. Hoden symmetrisch, in oder hinter der Körpermitte, längs gestellt. Ovar unmittelbar vor den Hoden, rechtseitig, [Except *Paragonimus westermanni* in which amphitypy occurs] meist stark gelappt [except Troglotrema]. Receptaculum seminis und Laurerscher Kanal vorhanden. Dotterstöcke meistens sehr stark entwickelt [except Collyriclum] und dabei ausschliesslich oder hauptsächlich unter der Rückenflächs ausgebreitet, nur einen medianen Streifen frei lassend. Uterus bald sehr lang und stark hin und her gewunden, bald relativ kürzer und mehr aufgeknaült. Eier im ersteren Falle klein, 0.017-0.025 mm lang, im letzteren bedeutend grösser, von 0.063-0.085, nach einigen Angaben sogar bis 0.12 (?) mm Länge.—Parasiten von carnivoren Säugetieren oder von Vögeln, meistens paarweise in cystenähnlichen Höhlungen."

This family appears to be an unnatural grouping. Of the four genera included three of them, Troglotrema, Paragonimus and Collyriclum, show radical divergence from the family diagnosis as evidenced by the fact that exceptions must be made in order to include them. In an appendix the author adds to this new family *Renicola pinguis* which he says is the closest relative of *Collyriclum faba*.

Jegen (1917) cites the close relationship of Collyriclum to *Brandesia turgida*. This author emends the family diagnosis of Odhner for the new family Troglotremidae as follows in order to include these two genera, Renicola and Brandesia. "Die Haut entweder mit spitzen Stacheln oder mit Schuppen durchsetzt. Bauchsaugnaf entweder unmittelbar vor oder hinter der Körpermitte."

The present investigations do not show the same close relationship for Collyriclum as found by Odhner and Jegen in the family Troglotremidae while it shows a distinct relationship to Brandesia. This genus is strikingly different from other genera in Odhner's family Troglotremidae.



Table II. Probable Relationships of Collyricidae

	<i>Brachycoelinae</i>	<i>Collyricidae</i>	<i>Pleurogenetinae</i>
Shape	Egg-shaped or spherical	Hemispherical	Small to medium slightly elongated
Integument	Naked rarely spinous	Spinous-in rows	Spiny or scaled
Oral sucker	Well developed	Terminal small	Weakly developed
Acetabulum	Well developed	Wanting	Weakly developed
Pharynx	Small	Smaller than sucker	Poorly developed
Crura	Thin, small	Thin, voluminous	Never reaching posterior end
Excretory	V-shaped	Large Y-shaped	V or Y-shaped
Genital pore	Ventral between suckers	Center of ventral surface	Between suckers, lateral
Copulatory organs	Present or absent	Present, moderately developed	Well developed
Testes	Symmetrical oval	Symmetrical, irregularly lobed	Symmetrical oval
Ovary	Lateral, near acetabulum	Lateral, anterior, deeply lobed	Lateral, near or anterior to acetabulum
Receptaculum seminis	Present	Wanting (?)	Present
Laurer's canal	Present	Present	Present
Vitellaria	Single arborescent group	Several arborescent groups on each side	Simple arborescent group anterior to crura
Uterus	Usually posterior to testes	In general in posterior body half	Usually in posterior body half
Eggs	Numerous about $22\mu$ long	Numerous 19 to $21\mu$ long	29 to $34\mu$ long 13 to $16\mu$ broad
Host	Mammals, birds and reptiles	Birds, parasitic in pairs in cysts	Amphibia and reptiles. Renicola and Loxogenes in pairs



The position of the genital pore as well as the organology depicts it as distinct from Collyriclum. This study confirms the systematic position of Brandesia given by Looss in that it is more closely related to the Pleurogenetinae. Collyriclum is in some respects closely related to the Pleurogenetinae and in other respects to the Brachycoelinae. The diagnostic characters of Collyriclum are so evenly distributed between these two sub-families that it holds an intermediate place as shown in the table opposite.

Whether the interpretation given above is the correct one remains indeed a matter of conjecture and certainly lacks much of confirmation. It is difficult to ascertain from an anatomical study of adult forms as to whether acetabula are vestigial. The most immature Cyclocoelidae studied by the writer show no trace of such organs. These forms belong to *Cyclocoelum obscurum*. In more advanced stages of *Cyclocoelum halli* the sucker is found practically as well developed as in the adult. Since the material of the immature stage of *Cyclocoelum obscurum* was not well preserved conclusions cannot be drawn from it. In the immature stages of *Notocotylus urbanensis* studied by the writer the ventral glands were found to develop after encystment of the cercariae and to show no relation in their development to an acetabulum. Much evidence on this point can yet be obtained by the elucidation of this and other life histories.

It is worthy of note, however, that in the Notocotylidae the oral sucker is well developed in the cercariae as well as in the adult, but instead of a single well developed acetabulum the condition is somewhat varied. In *Notocotylus quinqueserialis* five rows of small sucking discs are provided. In *Notocotylus attenuatum* three rows of similar organs are present, while in *Nudocotyle* and *Paramonostomum* no such sucking organs are present. These species live in a similar habitat (intestine of the muskrat) and under this condition have developed in the first instance different numbers of these organs while in the latter case no such structures have been observed. *Nudocotyle novicia*, however, presents other striking differences which need not be considered here. In the cercariae of these forms described notably by Cort (1914) and Faust (1918) no such organs are found nor is there any indication of their early development, while in the immature forms of *Notocotylus urbanensis* studied by the writer these glands are found well along in development soon after being freed from the cyst. The other organs of these cercariae correspond so well to the adult structure that there is little doubt as to the identity of the form. In this case then the sucking discs are developed after the organism enters the definitive host. A final decision of this question, however, must await further evidence and experimental demonstration of the life history.

The cases of reduction of sucking musculature cited by Cohn (1904) and Odhner (1907, 1911) lead again to the question raised previously and in the light of the theory of Cohn and Odhner it is difficult to determine

if this reduction is of phylogenetic import or subject to rapid change under environmental stimuli. A comparison of similar worms under different conditions leads to the belief that the sucking musculature is not subject to such rapid and radical change as indicated by Odhner (1907). As shown in an earlier part of this paper, *Cyclocoelum wilsoni* and *Cyclocoelum vicarium* from the intestine of their host have poorly developed oral suckers and no trace of an acetabulum while Cohn has found a rudimentary acetabulum in *Monostomum flavum*, a species which inhabits the trachea.

In the Heronimidae which inhabit the lungs and especially the larger bronchi of turtles, the oral acetabulum is well developed while any evidence of the presence of a ventral sucker has not been obtained. This stands in rather striking contrast to the statement of Odhner (1907) referred to above. Fuhrmann (1904) cites an interesting case in his *Bothriogaster variolaris* which was collected from the intestine of *Rostrhamus sociabilis*. This species according to the author has a ventral acetabulum but no oral sucker. A pharynx, however, is present. As stated previously his species is strikingly similar to *Monostomum oculobium* Cohn taken from *Vanellus melanogastrus* which Cohn (1902) says is devoid of sucking apparatus. Why has the oral sucker of *Bothriogaster variolaris* atrophied if reduction is due to habitat as stated by Cohn (1902) and Odhner (1907)?

Another interesting correlation is found among the Notocotyliidae and the Pronocephalidae both of which inhabit the intestine. Among the Notocotyliidae are forms which late in life develop the ventral holdfast or adhesive glands and those without such glands, both types of which have been found in the alimentary tract of the muskrat. Linton (1910) reports a species *Barisomum erubescens* from the intestine of three tropical fish which show no sign of any sucking organ save the oral. Of the several genera of the Pronocephalidae taken from the intestine of *Chelone midas* only *Adenogaster* shows any trace of accessory adhesive apparatus. On the other hand Odhner (1911) found reason to ally the Angiodictyidae a closely related family to the distomes on account of a weakly developed acetabulum found in *Haplorchis carhinus* Looss.

As was stated previously Odhner (1907) proved beyond doubt the presence of both pharynx and oral sucker in *Didymozoon scomбри* Tschbg. but found there no ventral sucker. Four years later Ariola (1906) asserts the *Didymozoon* nature of *Köllikeria* (*Distoma*) *okeni* (Kölliker) which he states is synonymous with *Monostomum fillicolle* Rud. In the Parona material reported as *Köllikeria* in which there were many distomes according to this author, he finds a single form without the acetabulum.

On the other hand *Collyriclum faba* (Bremser) and *Collyriclum colei* Ward, other cyst living trematodes, have no acetabula but present, however, a well developed oral sucker. It is difficult to interpret how worms which

live under such similar conditions as the Didymozoonidae and the Collyriclidae could by the effect of habitat alone become so totally different.

That the habitat in which the worm lives is a factor in the modification cannot be disputed but is certainly only one factor which contributes to the modification. What makes up the aggregate of factors in a given case could be only a matter of conjecture. Recent experimental investigation, however, has shown that factors influencing modifications of an individual or race may be both external and internal and that the change produced may be gradual or occur as a mutation in which case little or no trace may be left to depict the ancestral route. While the writer is inclined to look upon the loss of sucking musculature as a gradual change brought about by a group of factors among which the habitat seems to have played an important part, there is every reason to believe that sudden radical rearrangements have taken place and these are no doubt responsible for many of the variant forms. While there is good reason to believe that the Monostomata have arisen from highly divergent groups the evidence seems as yet about equally divided and the final decision must necessarily rest on further studies of the anatomy and life history of members of this and other groups.

The systematic arrangement used in the earlier part of this paper is essentially that employed by Lühe (1909), Kossack (1911) and Ward (1918), which for the above stated reason it seemed best to preserve at least for the present. It is hoped that interest in this aberrant group will increase and that careful studies will result either in the preservation of these forms as a natural taxonomic group or in their separation and subsequent distribution among other well organized units to which they are truly related.

## SUMMARY

- I. Monostomes from North American land and fresh water hosts have been studied.
- II. Nine new species have been described in detail.
- III. The knowledge of their anatomy and life history is greatly increased.
  1. Both oral sucker and pharynx are present in the Cyclocoelidae.
  2. In the genera of Cyclocoelidae studied the receptaculum seminis is a constant feature while Laurer's canal is not present.
  3. The origin of the ventral glands in *Notocotylus urbanensis* is clearly shown in early stages of development.
- IV. The discovery of well developed miracidia in *Collyriclum colei* renders improbable Jegen's account of the life history of *Collyriclum faba*.
- V. A careful study of the anatomy of the Cyclocoelidae, the Notocotylidae, the Collyriclidae, and the Heronimidae demonstrates clearly that they are not immediately related.
  1. The Cyclocoelidae are probably allied to the Fasciolidae.
  2. The Notocotylidae are closely related to the Pronocephalidae not merely in general organology but especially in the presence of peculiar ventral glands.
  3. A study of the organology of the Collyriclidae demonstrates clearly their direct relationship to the Pleurogenetinae.
  4. The Heronimidae do not show immediate relationship to any known trematodes.
- VI. The monostomes are a heterogeneous group and must ultimately be distributed among other groups in accordance with their fundamental relationships.



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## DESCRIPTION OF PLATES

## LIST OF ABBREVIATIONS

<i>c</i> cirrus	<i>ov</i> ovary
<i>cm</i> circular muscle	<i>p</i> pharynx
<i>cp</i> cirrus pouch	<i>pp</i> prepharynx
<i>g</i> ventral glands	<i>rs</i> receptaculum seminalis
<i>ga</i> genital atrium	<i>ru</i> receptaculum seminalis
<i>i</i> intestinal crura	uterinum
<i>lm</i> longitudinal muscle	<i>sg</i> shell gland
<i>m</i> mouth	<i>u</i> uterus
<i>o</i> ootype	<i>v</i> vas deferens
<i>e</i> esophagus	<i>vd</i> vitelline duct
<i>om</i> oblique muscle	<i>vr</i> vitelline reservoir
<i>os</i> oral sucker	<i>w</i> wall of excretory tubule

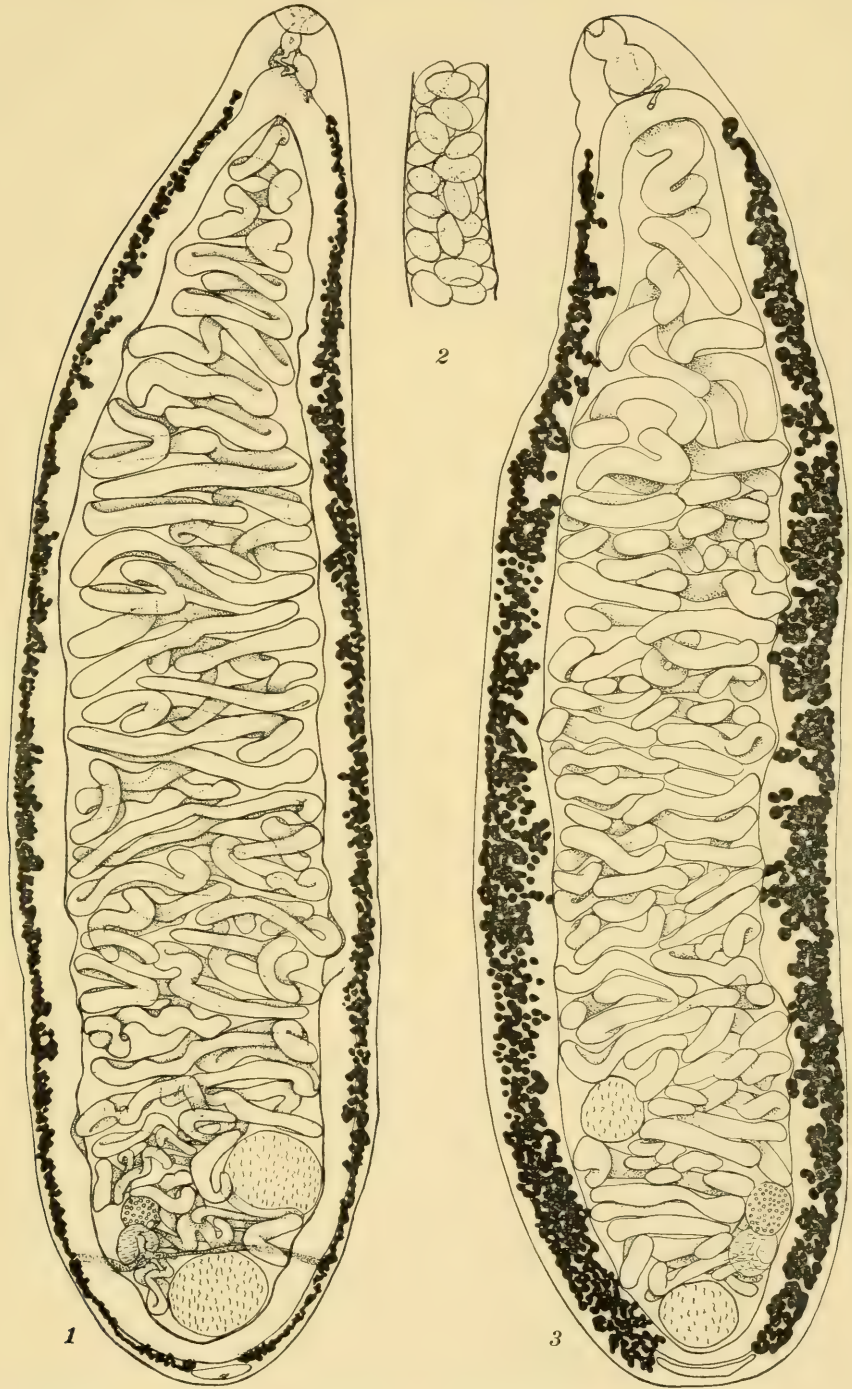
All drawings were made by the aid of either a camera lucida or an Edinger drawing apparatus.

## PLATE I



## PLATE I

- Fig. 1. *Cyclocoelum leidyi*, dorsal view.  $\times 12$ .  
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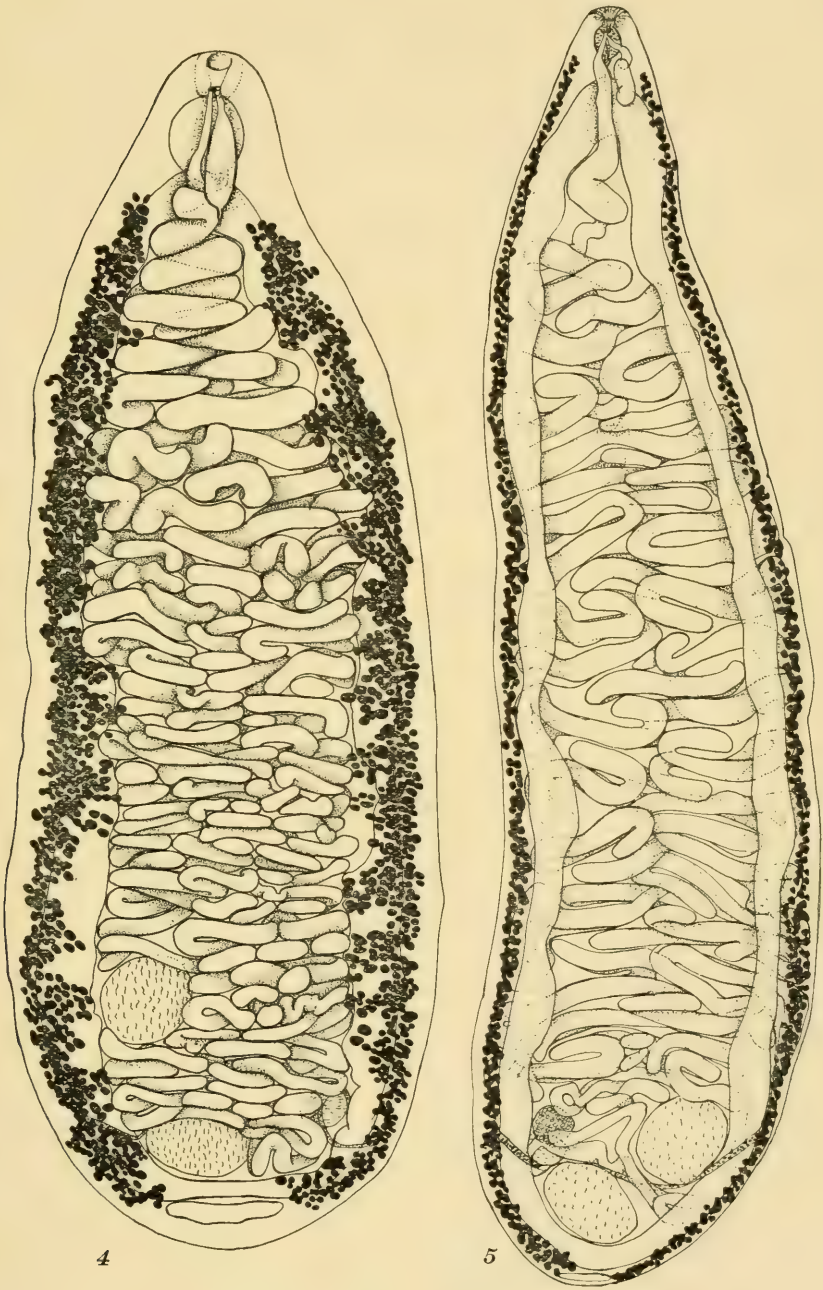


## PLATE II



## PLATE II

- Fig. 4. *Cyclocoelum pseudomicroslomum*, ventral view.  $\times 12$ .  
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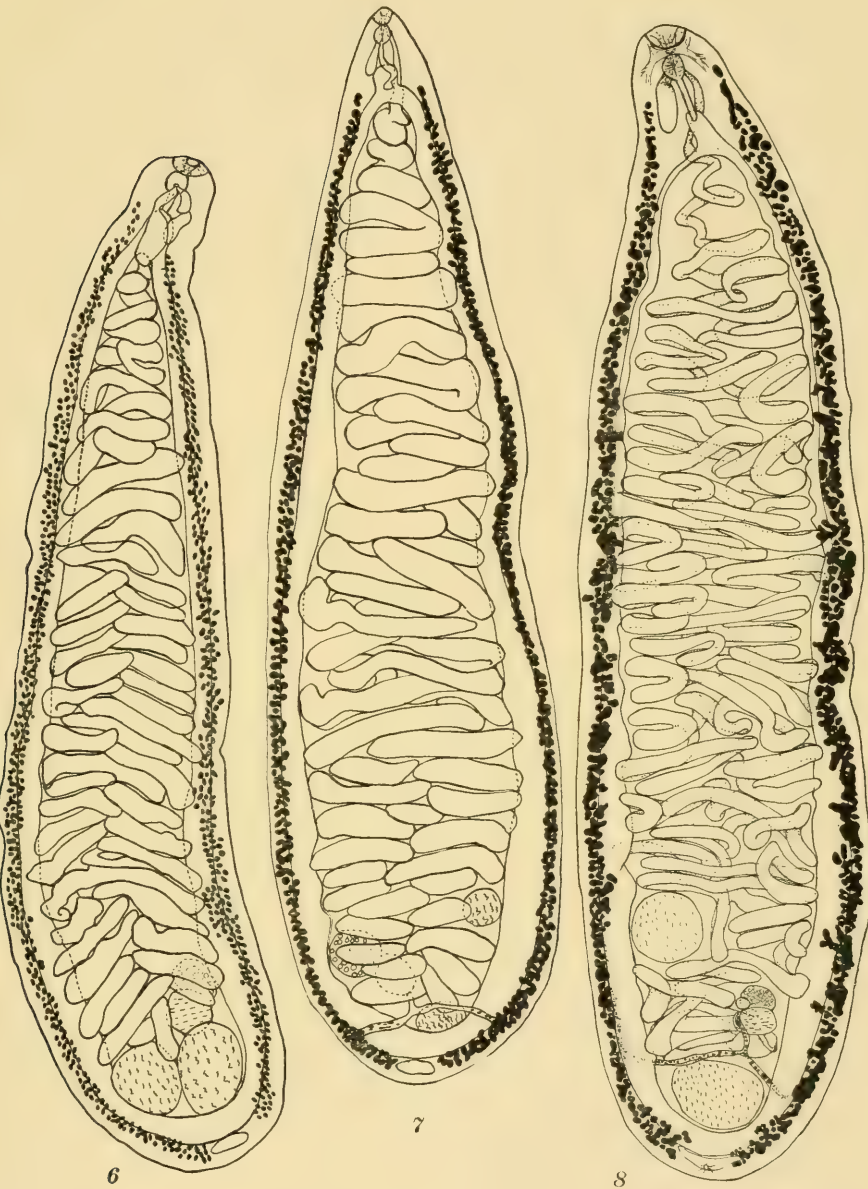


## PLATE III



## PLATE III

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## PLATE IV

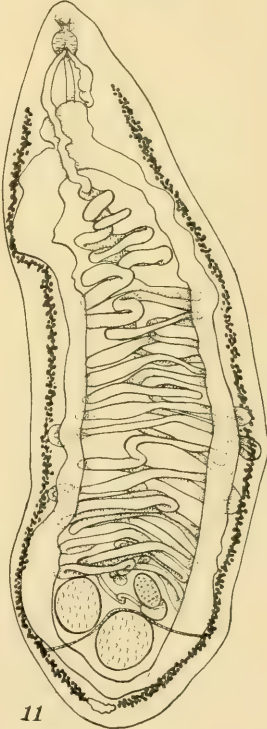
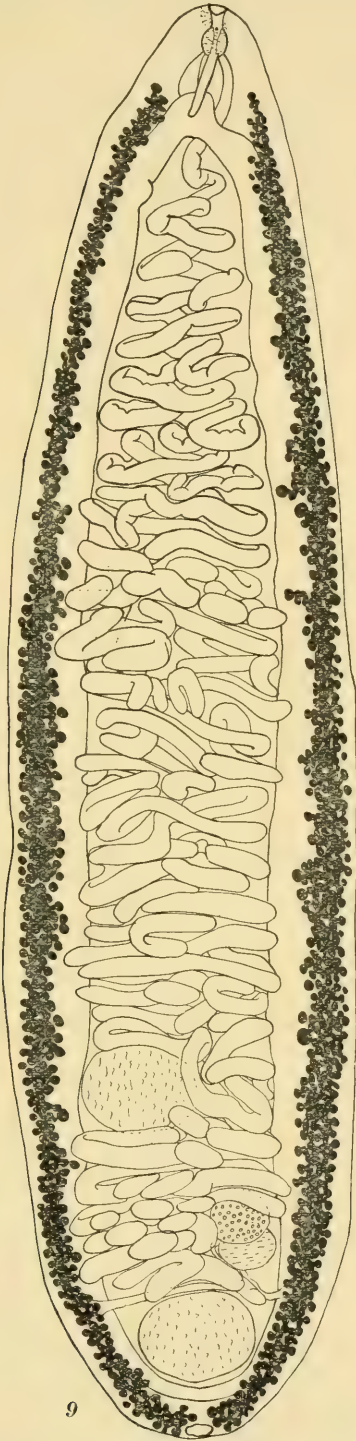


## PLATE IV

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Fig. 11. *Cyclocoelum halli*, young specimen, ventral view.  $\times 23$ .



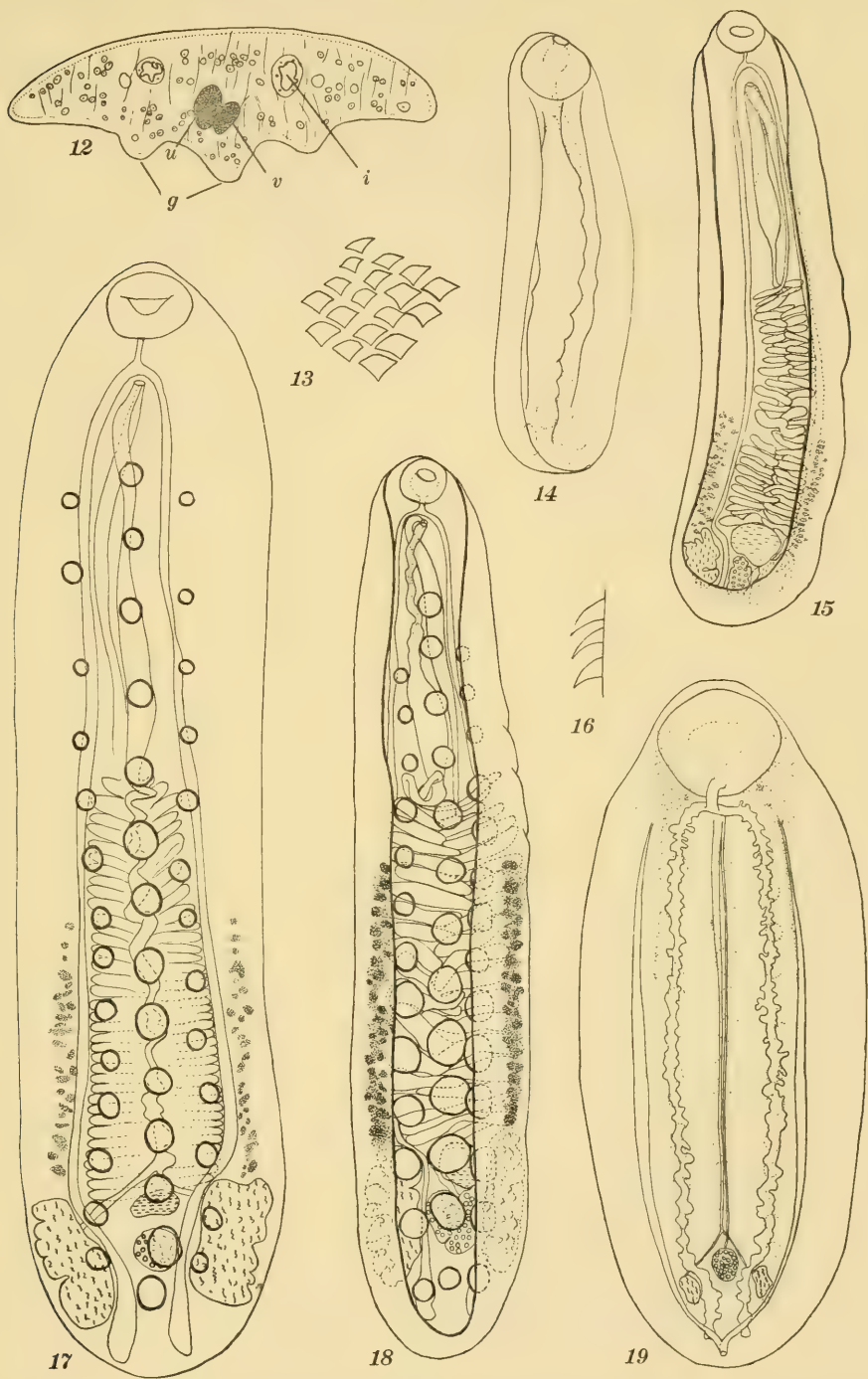


## PLATE V



## PLATE V

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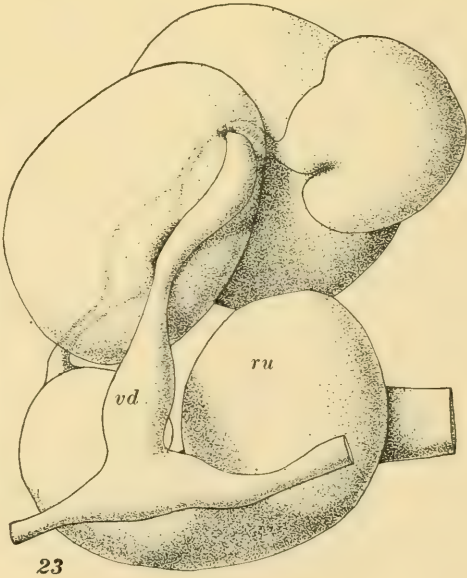
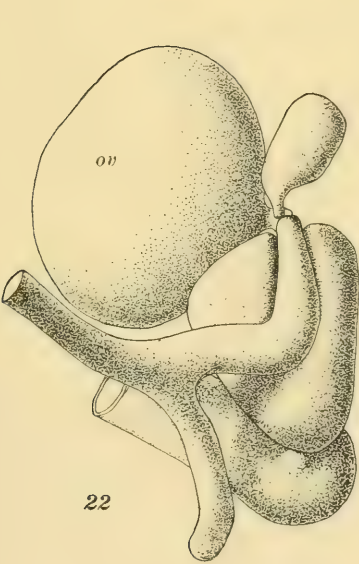
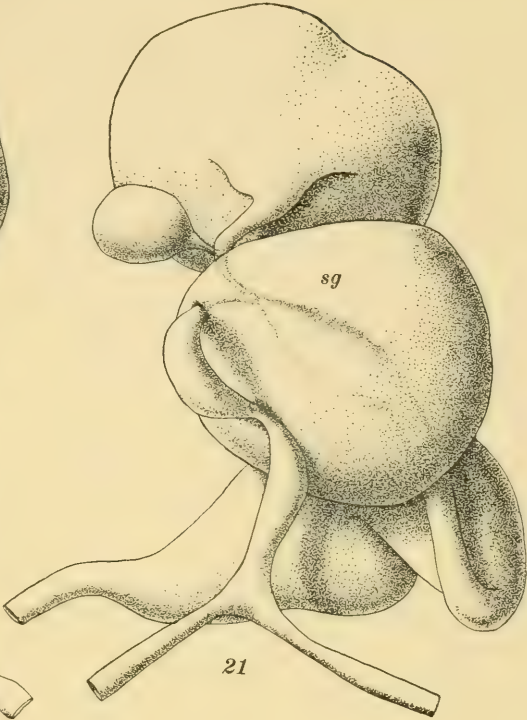
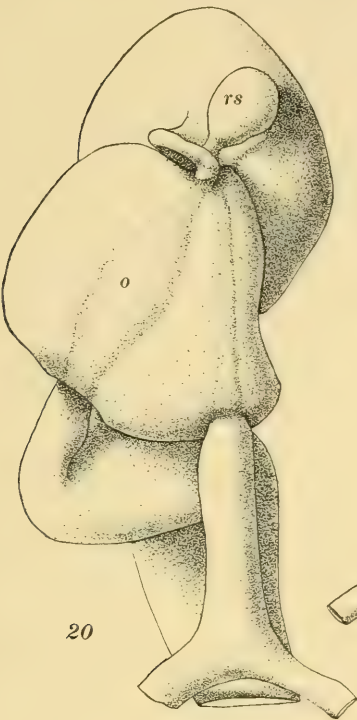
## PLATE VI



## PLATE VI

All figures magnified 92 times

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- Fig. 22. Ovarian complex *Cyclocoelum obliquum*, drawing from wax reconstruction.
- Fig. 23. Ovarian complex, *Cyclocoelum problematicum*, drawing from toto mount of No. 2449 Berlin Museum.



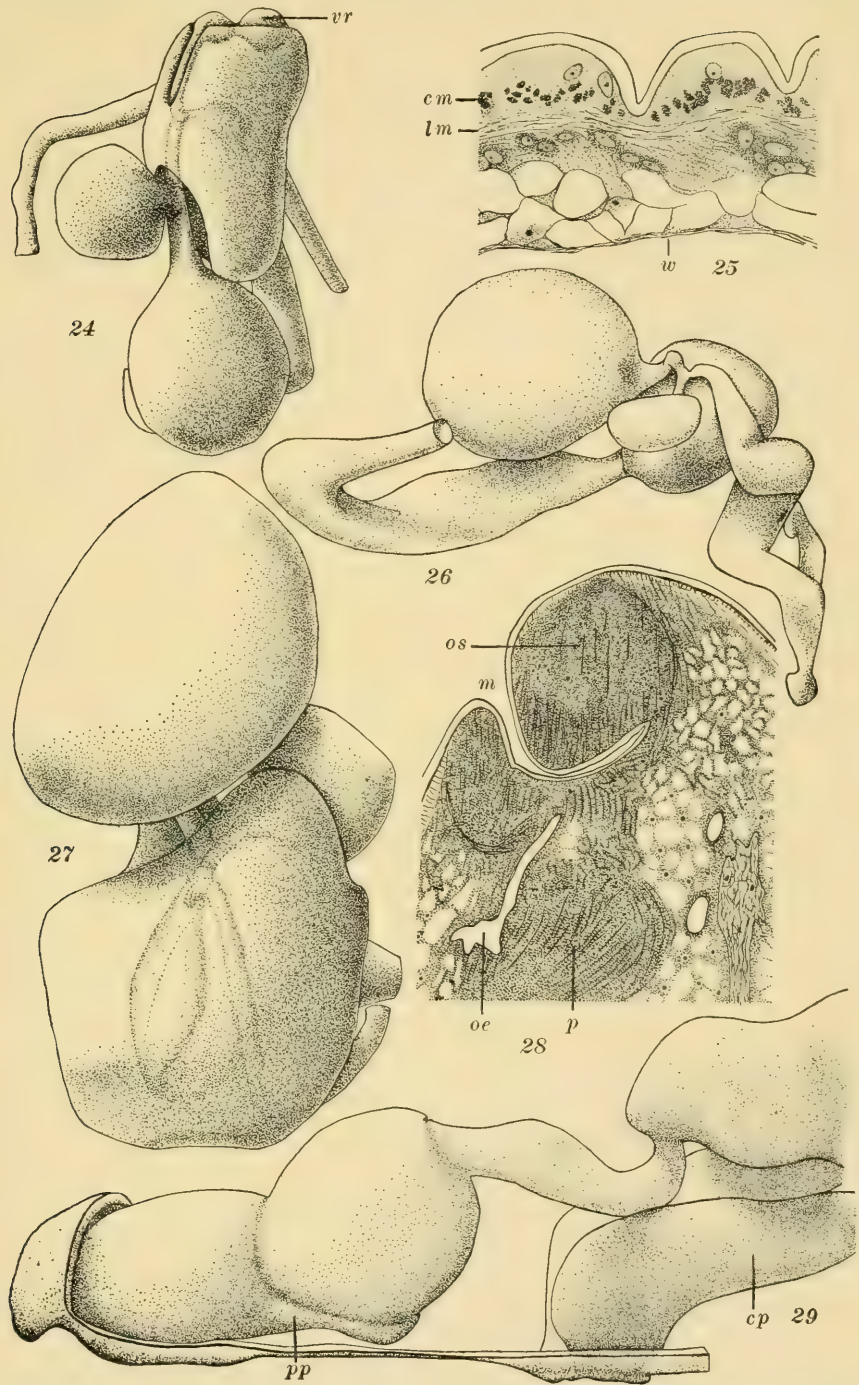


## PLATE VII



## PLATE VII

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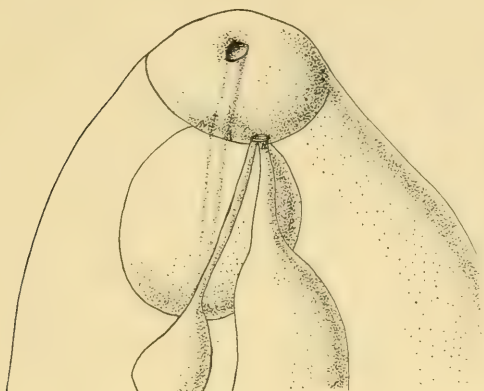
## PLATE VIII



## PLATE VIII

All figures magnified 44 times

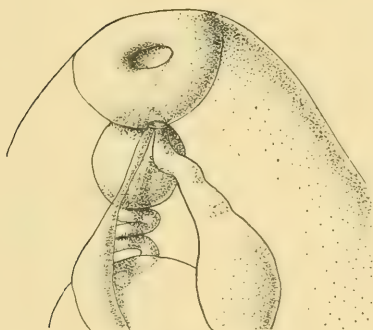
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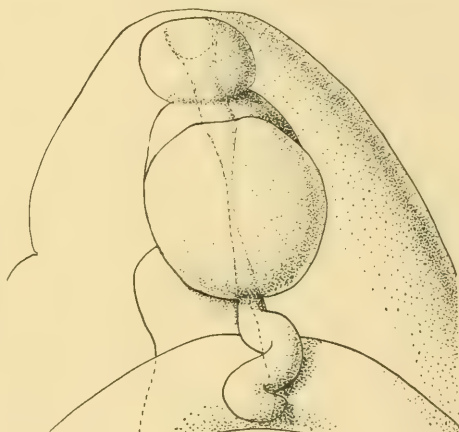
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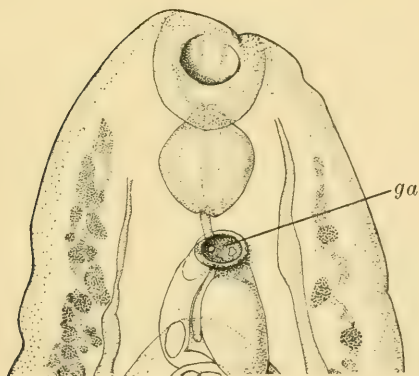
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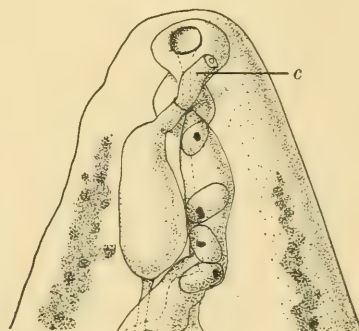
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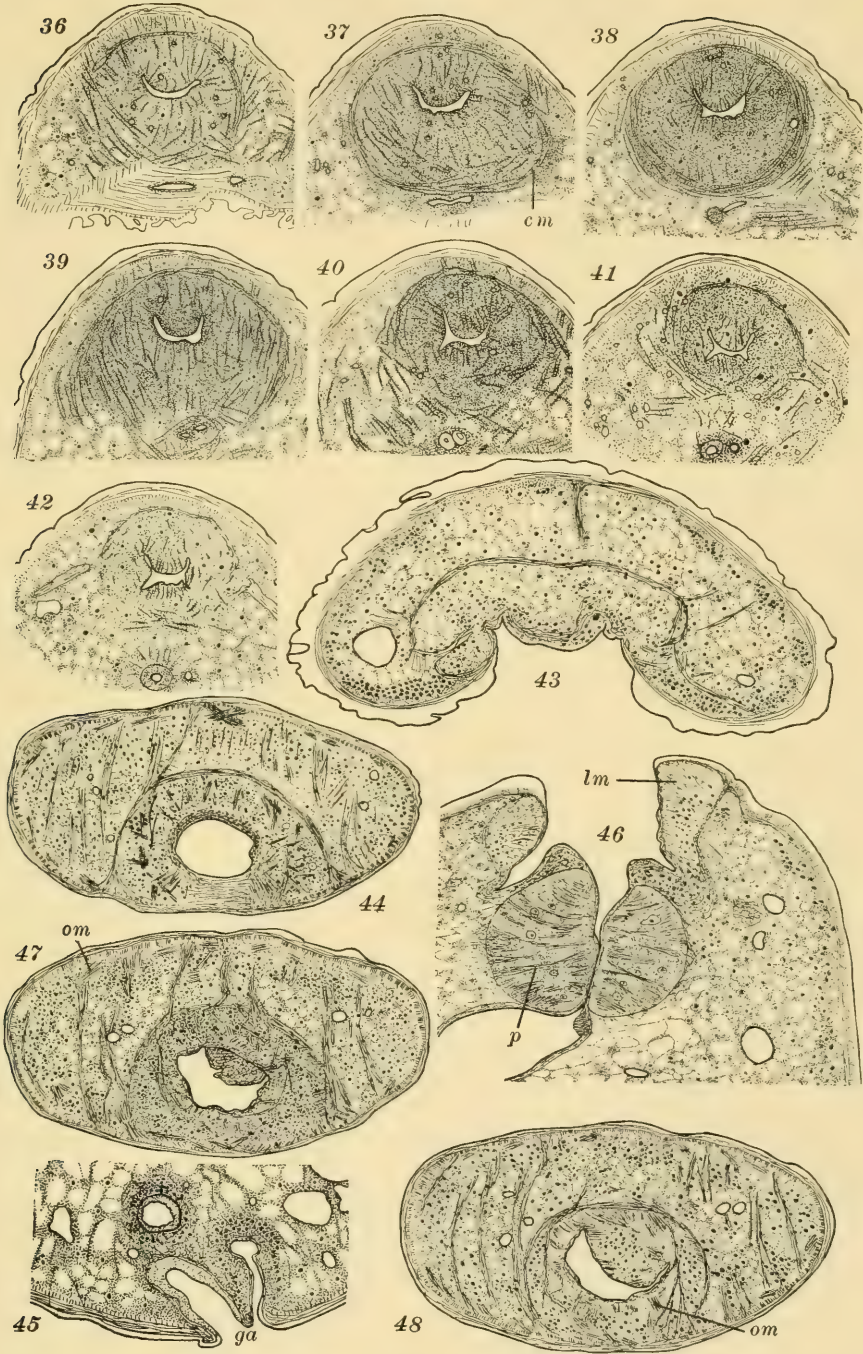


## PLATE IX



## PLATE IX

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A CLASSIFICATION OF THE LARVAE  
OF THE TENTHREDINOIDEA

WITH FOURTEEN PLATES

BY  
HACHIRO YUASA

Contributions from the  
Entomological Laboratories of the University of Illinois  
No. 69

THESIS

SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE  
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SCHOOL OF THE UNIVERSITY OF ILLINOIS

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## I. INTRODUCTION

That the cardinal principle of modern taxonomy is based on the fundamental facts of evolution and that the essential problem of classification is the phylogenetic relationship of organisms need no argument. In order to ascertain genetic affinities, it is not sufficient to investigate the morphological characters alone, but all other attributes, physiological and biological, must be considered. It is also evident that the immature stages of organisms should receive as thoro consideration as the adult if taxonomy of insects is to attain that degree of comparative perfection obtained in the classification of other organisms.

Systematic entomologists, dealing as they do with animals of such diversity and complexity morphologically and biologically, have from early times recognized, at least to some extent, the taxonomic significance and value of the developmental stages of insects, but the practical difficulties in obtaining necessary materials, accurately determined and adequate in quantity and range, have made progress in this phase of insect taxonomy very tardy. A good start, however, has been made by recent workers as was pointed out by Brues (1919), and their results vindicate both the possibility and practicability of such investigations. There is, moreover, an urgent demand for such studies from economic entomologists, who are constantly confronted by the problem of identifying the immature stages of economic species.

The present study is an attempt to deal with the larvae of the Tenthredinoidea from the standpoint of synoptic and, to some extent, genetic classification. The systematic significance of the morphological characters will be discussed in part two; the taxonomic treatment of the families, subfamilies, genera, and species will constitute part three; and, as full a discussion of the phylogenetic relationship of the families as is possible with the data at hand, will form part four. No one appreciates the inadequacy of this study, both in thoroughness and comprehensiveness, more than the author, but it is hoped that he has opened a way for those who will advance our knowledge of this highly interesting group of insects to a more satisfactory condition in the future.

The taxonomic literature dealing with the adults of the Tenthredinoidea is extensive. The historical development of the subject is interesting to students of this group of insects but a detailed account is out of place here. However, a brief statement of the history of the group is desirable.

Linnaeus in the fourth edition of the *Systema Naturae* (1744) established the order Hymenoptera under the name of Gymnoptera and applied to the order its present designation in the first edition of the *Fauna Suecica*. The name *Piezata* was proposed by Fabricius (1775) for the order, but this name never came into general use. Latreille (1796), following Linnaeus, divided the order into two sections, Terebrantia and Aculeata. The first section included two groups, Phytophaga, which comprises the Tenthredinoidea, and the Entomophaga or parasitic Hymenoptera. The *Ditrocha* and *Monotrocha* of Hartig (1837) correspond approximately with the two sections of Latreille. Gerstaecker clearly recognized the Tenthredinoidea as a unique compact group and proposed in 1867 to divide the order Hymenoptera into two suborders. He used the name Symphyta for the Tenthredinoidea and Apocrita for the remainder of the order. The term Symphyta thus antedates Konow's (1890) subordinal name Chalastogastra. Various terms have been proposed for this group of Hymenoptera and the following are coextensive with the superfamily name Tenthredinoidea as used in the present paper: Phytophaga, Sessiliventre, Securifera, Serrifera, Symphyta, and Chalastogastra. Rohwer and Cushman (1917) proposed a third suborder of Hymenoptera, Idiogastra, for the family Oryssidae and placed it between the Chalastogastra and Clistogastra of Konow.

Early students of the Tenthredinoidea divided the superfamily into two groups, Phyllophaga for the Tenthredinidae or "Tenthredo" of Linnaeus and Xyllophaga for the Siricidae or "Urocerus" of Geoffroy. With the exception of Stephens (1835) and André (1879), who recognized the additional families Xiphydriidae and Cephidae, respectively, besides the two families mentioned above, the old system was followed for many years. With the progress in studies of the world fauna of this group of insects, modern writers have proposed many elaborate schemes of classification. Konow in 1890 suggested one family and three subfamilies and Dalla Torre (1894) catalogued one family divided into eighteen subfamilies, while Ashmead (1898) proposed fifteen families and twenty-seven subfamilies. Enslin (1911) criticized Konow's three divisions as unnatural and proposed four families, Oryssidae, Siricidae, Cephidae, and Tenthredinidae, thus reverting to a considerable extent to the scheme of the old school as represented by Cameron (1882) and others. The recent and more important systems are those proposed by Konow (1905), MacGillivray (1906), and Rohwer (1911). These systems, when compared, show a great discrepancy in the number and rank of the groups which formerly constituted the family Tenthredinidae, as is indicated graphically in Plate XIV. MacGillivray, whose classification is based on a thoro-going phylogenetic study of the wings, is of the opinion that the large complex of genera obtained in this family are readily separable into a number of



definite groups on structural differences, and that they are best dealt with by considering them simply as subfamilies. In general the systems of Konow and Rohwer are, with the exceptions noted below, more in accordance with each other in their essential features than either one of them is with that of MacGillivray. A comparison of these three schemes brings out various points of interest. As far as the major groups are concerned, (1) all are in agreement in associating Xiphydriidae with Siricidae; (2) Konow and Rohwer agree in placing Siricidae and Siricoidea closer to Lydidae and Megalodontoidea respectively than does MacGillivray, as also in associating Megalodontidae with Pamphiliidae and Xyelidae and Pamphiliidae with Cephidae; (3) Konow and MacGillivray agree in the relation of the Blasticotomidae to Xyelidae and Pamphiliidae; (4) Rohwer differs radically from them in his arrangement of the Blasticotomidea, which he places between the Argidae and Tenthredinidae in his superfamily Tenthredinoidea; and, finally (5), Rohwer (1917) is unique in creating a third suborder of Hymenoptera, Idiogastra, for the Oryssidae. In respect to the arrangement of the subfamilies and tribes of the Tenthredinidae, as restricted by MacGillivray, the striking dissimilarity of these authorities in assigning different rank to more or less related groups is well illustrated in their treatment of the Emphytinae, Selandriinae, and Lycaotinae. According to MacGillivray Konow's tribe Selandriades of his family Tenthredinini corresponds to the three subfamilies just mentioned, while according to Rohwer it embraces not only these subfamilies but also another—Allantinae; that is, Rohwer considers the Emphytinae related to the Tenthredinidae thru the tribe Allantini, which, together with the tribes Taxonini and Eriocampini, constitute his subfamily Allantinae. The Emphytinae and Lycaotinae are also related, according to Rohwer, to the Blennocampinae thru his subfamily Empriinae, which contains, besides Empriini and Lycaotini, the tribe Blennocampini. MacGillivray and Rohwer agree in regard to the Cimbicinae to the extent that they both consider it a compact group. Konow differs radically from these writers by associating his tribe Syzygoniides with the Cimbicides and Abiides. In regard to Konow's Nematides and Lobocerotides, the three systems agree fairly well. The affinities of the Blennocampinae, Fenusinae, and Scolioneurinae are recognized by MacGillivray and Konow. Rohwer and Konow agree, as do all other systematists except MacGillivray, in treating the Diprioninae and Monocteninae as allied groups inseparable into subfamilies. Konow's subfamily Lophyrini, however, is a heterogeneous group and includes such widely separated groups as Acordulecerinae and Diprioninae.

The classification proposed by MacGillivray is based upon a critical investigation of an essential structure, the wing, and is a logical conclusion of the application of the taxonomic principles promulgated by Comstock



(1893). This system of classification is adopted in principle in the present paper, for the writer believes that by judicious discrimination between the palingenetic and the cenogenetic peculiarities, the characters manifested by immature insects may be interpreted as indicating the genetic affinities of the insects under consideration, and that in this sense the immature stages of insects are of systematic importance. A classification based upon such larval characters should agree in essential points with that based upon the adult characters chosen for their phylogenetic value, and therefore it is interesting to see whether MacGillivray's alary system is justified by a study of the larvae. It must be stated here that Dr. MacGillivray does not accept all my conclusions as to the relation of the families based upon a study of the larvae.

The immature stages of the Tenthredinoidea of more common occurrence seem to have attracted the attention of naturalists from an early time. In Moufet's *Theatrum Insectorum* (1634) the adult saw-flies are referred to the group "Vespa" and what seems to be a *Tremex* to "Odonata," but no mention of the larvae is made. Goedart (1682) was the first naturalist to make observations on the larvae of a saw-fly. His records, rendered in interesting archaic terms, clearly indicate that he had under observation the larvae of *Cimbex* or *Trichiosoma* on *Salix*, and *Arge* on *Rosa*. Madame Merian (1730) pictured saw-fly larvae together with those of the *Lepidoptera*, as may be seen on her plates 22, 25, and 33. Swammerdam's (1737) figure 1, table XLIV, refers to galls on the leaves and stems of *Salix* apparently made by *Pontania* or *Euura*. He also figured a larva having fifteen segments with larvapods on abdominal segments 3-8 and 11. Frisch (1766) figured about seven species and recorded observations on their life-history. De Geer, as cited by Bergmann, on the authority of Le Peletier (1823), had seen a larva with twenty-two feet exclusive of the anal larvapods. According to the same authority, Reaumur observed certain larvae with twenty-four feet, indicating a xyelidan condition. Linnaeus (1758) recorded the food-plants of twenty-two species of saw-flies out of the forty species of "Tenthredo" enumerated, and spoke of the larvae in general of "Tenthredonis larvae pleraeque folia plantarum exedunt, polypodae, seu pedibus plus quam XVI communiter instructae." Following Linnaeus many students of the Tenthredinoidea contributed much to a knowledge of the immature stages, altho quite disproportionately to their larger contributions to that of the adults. Among those who have done much towards the progress of our knowledge of the larvae, either as original investigators or as compilers or as both, the following are the more important: André, Brischke, Cameron, Costa, Dahlbom, Dalla Torre, Dufour, Dyar, Fallen, Hartig, Kaltenbach, Kirby, Klug, Konow, Latreille, Leach, Middleton, Newman, Oliver, Panzer, Le Peletier, Snellen von Vollenhoven, Spinola, Westwood, and Zaddach.

Still, our knowledge of the immature stages of the Tenthredinoidea is very meager in comparison to that of the adult. The larvae of only 418 species out of the total of 2701 species listed by Konow in his monograph (1905) were dealt with in his artificial table for the larvae. This was less than sixteen per cent of the described species of the world up to his time, and many larvae included in this sixteen per cent were known to this authority only thru literature. According to Dyar (1895) less than twenty-five per cent of the North American species have been recognized in the larval state. It is no exaggeration to say that the larvae of more than eighty per cent of the Nearctic species are yet to be described.

Our knowledge of the physiology and morphology of the immature stages of the Tenthredinoidea is exceedingly meager. The following list includes most of the important literature: Graber (1890) on the embryology of *Arge berberides*; Doncaster (1907) on the gametogenesis and fertilization in *Nematus ribesi*; Büchner (1918) on the accessory chromosomes in *Tenthredo*, *Allantus*, *Arge*, etc.; Frenzel (1885) on the epithelial regeneration of the alimentary canal of the larva of *Cimbex*; Holtz (1909) on the histology and physiology of the digestive cells in the larva of *Nematus*; Poletajew (1885) on the silk-glands of the larvae of *Cimbex* and *Tenthredo*; Cholodkovsky (1897) on the blood and reflex bleeding of the larva of *Cimbex*; and MacGillivray (1913) on the general external anatomy of the larvae.

The biology of the Tenthredinoidea abounds in phenomena of great interest to experimental evolutionists and presents many problems of ecological importance. The list of papers dealing with the life-history and habits, especially of economic species, is fairly extensive. Cameron (1882) has published an excellent summary of general biological and ecological observations. The biology of the Nearctic Tenthredinoidea has been discussed in detail by MacGillivray (1913). Since the biological and ecological studies of the Tenthredinoidea are beyond the scope of the present paper, readers are referred to the last-mentioned publication.

*Materials.*—Four collections, designated for convenience as the Cornell, Maine, MacGillivray, and Yuasa collections, contain most of the materials used in this study. The writer has examined more than 2500 alcoholic specimens of larvae representing at least 400 species during the course of this study. He has also, during the last few years, at Ithaca, N. Y., and at Urbana, Ill., made observations on the life-history and habits of numerous species in his attempts to breed more than two hundred and fifty species.

The Cornell collection consists of about forty species and belongs to the Cornell University. Most of the specimens were collected by Dr. MacGillivray and Mr. Chester Young in the vicinity of Ithaca, N. Y. They were in rather a poor state of preservation and proved useful only

in checking up materials in other collections and in comparing the descriptions of Young with his own material. This collection is designated by the letter C.

The Maine collection consists of about 200 species, many of which were bred and identified by Dr. MacGillivray. The collection belongs to the Maine Agricultural Experiment Station and all the specimens were in excellent condition. They were collected by Dr. MacGillivray with the assistance of Mr. Earl Shaw during the summer of 1913 in the vicinity of Orono, Maine. This collection together with the collecting and breeding records were placed in the writer's hands, and they proved to be indispensable to the present study. The collection is designated by the letter M.

The MacGillivray collection consists of about thirty-five species collected and identified by Dr. MacGillivray, together with larvae of some unidentified species. The specimens came from Ithaca, N. Y., Orono, Me., Onekama, Mich., Urbana, Ill., and a few other localities. This collection is designated by the letter G.

The Yuasa collection consists of about two hundred and thirty species including 98 bred species. A majority of the specimens were collected by the writer at Ithaca, N. Y., during the summers of 1917 and 1918. Some species were collected at Urbana, Ill., and others came from different parts of the United States and Canada thru the generosity of various entomologists. This collection contains also the cocoons of practically all the bred cocoon-making species and eggs and pupae of a limited number of species. This collection is designated by the letter Y.

Besides the four collections just mentioned, a number of rare specimens were generously loaned to me by several people, as subsequently acknowledged, and were of great value in the preparation of this paper.

*Identification.*—All bred species in the Maine, MacGillivray and Yuasa collections were identified by Dr. MacGillivray. Some of the specimens in the Cornell collection bore labels, and when the larvae agreed satisfactorily with the published descriptions the identifications were accepted. In only a few cases has identification depended solely on published descriptions of larvae.

*Terminology and Nomenclature.*—For the description of the external anatomy of the head and mouth-parts of the larvae the terms used in my paper (1920) dealing with the generalized insects have been used. Other terms, some new, are used in part II. Taxonomic names have been adopted from Rohwer (1911) and MacGillivray (1906).

*Bibliography.*—Works on taxonomic units are omitted altogether. A complete bibliography of the Nearctic Tenthredinoidea was not undertaken owing to space limitations, but the most important literature on the subject is listed, as also that cited in the text.



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## II. MORPHOLOGY

The external anatomy of the larvae of the Tenthredinoidea has received but little attention from entomologists. The only important contribution on the subject is MacGillivray's study (1913), which deals with the anatomy and coloration as well as with the biology of the larvae. The writer has made a comparative study of the external anatomy of the larvae of representative Nearctic Tenthredinoidea in order to find characters upon which both analytic and synoptic classifications of the larvae might be based. Since MacGillivray has treated the general aspect of the anatomy, only the more important structures and features will be discussed in the following pages.

The larvae of the Tenthredinoidea (Figs. 1-25) are typically subcylindrical, eruciform, caterpillar-like, slightly flattened on the ventral aspect, and usually taper slightly caudad. In the leaf-miners the body is depressed. The body in its metamerism is well differentiated into a head and a series of thirteen somites which are more or less similar in structure. The segmentation is distinct. The first three segments compose the thorax and are distinguishable on account of their position, form, and, in podous larvae, more readily by the presence of three pairs of thoracic legs. The abdomen consists of the ten remaining visible segments and in polypodous larvae the presence of larvapods gives a characteristic appearance to the uromeres. They are usually subdivided by transverse depressions into annulets.

*Head.*—The head (Figs. 26-38) is typically subglobose, more or less circular in frontal contour, strongly chitinized, and usually setiferous. The mouth is directed ventrad or slightly ventro-caudad. In the leaf-miners it is directed cephalo-ventrad as in the Fenusinae (Fig. 34) or cephalad as in Phlebotrophia (Fig. 37). The surface of the head may be polished and shiny as in *Neodiprion* (Fig. 28), or roughened, verrucose, or granulate, and divided into minute irregular areas as in *Pteronidea* (Fig. 30) and the *Cimbicinae* (Fig. 29), or, in life, thinly coated with a waxy secretion, as in some *Emphytinae*. It may be glabrous as in *Metallus* (Fig. 35) and *Phlebotrophia* (Fig. 37), or it may be variously setiferous as follows: microscopically and sparsely setiferous as in *Tremex*; with a few scattering setae as in the *Phyllotominae*; with minute stiff peg-like setae as in *Neodiprion*; with numerous promiscuously distributed short setae as in *Dolerus*

and the Tenthredininae; with long setae as in Pteronidea; or with abundant conspicuous setae as in Monophadnoides and the Cladiinae. The setae tend to be more numerous and longer on the ventral portion of the head. The number and location of the setae on the head vary with the individuals, excepting those on the clypeus and labrum, but their general characteristics, such as relative abundance, manner of distribution, and the kind of setae, are constant within genera and subfamilies. The head may be pale, creamy white, or light brown, but often in life appears as green or greenish white on account of the greenish blood showing thru the cuticle, or it may be blackish or brownish with or without distinct color-markings. The darker color is due to a deposition of colored pigments in the cuticle and is generally permanent in alcoholic specimens. The color and the coloration of the head are generally constant specific characters. There are, however, ontogenetic changes in these respects. The very young stages may be lighter in color and later stages darker, or vice versa as in *Cimbex*, or all stages except the last instar may be darker and the ultimate stage greenish as in *Pteronidea ribesii*. The color markings may be diffuse in the young and become localized and definite in older stages, as in some species of *Dolerus*, or they may vary from faint spots to general contiguous markings as in certain species of *Strongylogaster*. The more common markings are brownish spots on the dorsum of the vertex, on the front, and often caudad of each ocellera. There may be a stripe along the epicranial stem and vertical furrows or dorsad of the ocellaræ. When the head is darkly colored the clypeus is usually lighter in color than the other parts of the head.

The head is usually exposed, but there is a tendency in the leaf-miners, wood-borers, and a few others to have the cephalic end of the prothorax produced into a broad fold on the dorsal and lateral aspects. This fold covers the caudal portion of the head as in *Tremex*, *Metallus* (Fig. 35), and *Caliroa* (Fig. 69).

The structures of the head will be discussed under two sections, one dealing with the fixed parts, that is all the immovable parts of the head-capsule, and the other dealing with the movable parts—the antennae and mouth-parts. The fixed parts include the vertex, front, clypeus, labrum, occiput, and postgenae, together with their bounding sutures, ocellaræ, and tentoria.

*Epicranial Suture.*—The inverted Y-shaped median suture of the head is the epicranial suture. The stem (*es*) of the Y originates at the occipital foramen, extends cephalad, dividing the vertex into halves, and bifurcates on the cephalic aspect of the head. Each arm of the bifurcation (*ea*) extends obliquely laterad for a short distance and then bends ventrad to the ventral margin of the head, terminating near a precoila. The epicranial suture is present in all larvae except those of the Xiphydriidae

(Fig. 45), where it is in part indistinct, and in the Siricidae and Oryssidae, where it is obsolete. It is interesting to note that the most highly specialized genus of the Tenthredinidae, *Phlebotrophia* (Fig. 37), possesses this suture. The relative length of the stem and arms varies in different families and subfamilies. There is a depression near the bend of the arm, as in *Lygaeonematus* (Fig. 31), which indicates the point of attachment of muscles (*ma*), and should not be confused with a true tentorina (*pn*). Near the ventral end of each epicranial arm there is a thickening of the surface and a pit. This pit is a pretentorina (*pn*) and the thickened piece corresponds to the clypealia (*cl*) of the larva of *Corydalis*. The pretentorina and clypealia are constant in position and universal in occurrence in the Tenthredinoidea. In the Siricidae the pretentorinae are distinct and sometimes mistaken for ocellaræ. In ecdysis the head is split along the epicranial suture nearly to the ventral ends of the arms.

*Vertex*.—The large area on each side of the epicranial stem is the vertex (*v*). It extends from the dorso-meson of the epicranium to the ventral margin of the head, laterad of the epicranial arm, and cephalad of the occipital suture when this is present, and bears an ocellara (*o*) and antennaria (*ar*). There is on the dorsal part of the vertex on each side a distinct furrow which originates at the occipital foramen and extends cephalad for some distance onto the lateral aspect of the head. This is the vertical furrow (*vf*) and is characteristic of the larvae of the Tenthredinoidea. It is wanting only in the leaf-miners and wood-borers. The nature of this furrows is not known. There is a corresponding carina on the ental surface of the head, and the major muscles of the retractor of the mandible are attached to the ental surface of the vertex dorsad and ventrad of the vertical furrow. The furrows usually converge at the cephalic end, but sometimes are subparallel to each other.

*Genæ*.—The portion of the vertex ventrad of an imaginary line drawn ventrad of each ocellara parallel to the ventral margin of the head is a gena (*g*). The extent of the genæ varies, therefore, according to the location of the ocellaria. The setae on the genæ are sometimes longer than those elsewhere.

*Ocellaria*.—The larvae of the Pamphiliidae, Xyelidae, Tenthredinidae, and Cephidae possess a pair of ocellaræ (*e*), one on each side of the head. These organs of sight are remarkably uniform and constant in structure and location. With the exception of *Phlebotrophia* and the Cephidae, the ocellaræ are usually clear, semiglobose or at least distinctly convex, and are located on or near the center of the ocellaria (*ou*), which are usually circular and distinctly blackish. The ocellaria are located on the vertex dorsad of the antennariae in the Tenthredinidae and caudad of them in the Pamphiliidae and Cephidae. In the Cephidae and *Phlebotrophia* the ocellaria are obsolete and the ocellaræ are indicated by pigmented



granules showing thru the cuticle. The ocellaræ are obsolete in the highly specialized families, Xiphydriidae and its allies. The life-habits are correlated with the presence and the degree of development of the organs of sight.

*Front.*—The area bordered by the epicranial arms on the cephalic aspect of the head is the front (*f*). The ventral boundary is indicated by a transverse depression connecting the ventral ends of the epicranial arms. This depression is the fronto-clypeal suture (*fcs*). The depression is usually concave dorsad and often obsolete at each lateral end. The front is usually flattened or only slightly convex and bears scattered setae which vary in number and arrangement in different genera and in arrangement in different individuals. The extent of the front is determined by the length of the epicranial arms. The front is usually subquadrate, often wider than long, but in some cases, as in *Caliroa* (Fig. 53), it is much longer than wide. In the absence of the epicranial stem the lateral boundaries are indicated by the pretentorinae as in *Tremex* (Fig. 46). *Phlebotrophia* (Fig. 37) is unique in possessing a distinct median longitudinal furrow on the dorsal half of the front.

*Clypeus.*—The area ventrad of the front is the clypeus (*c*). Its ventral boundary is the clypeo-labral suture (*cls*), and the lateral margins are free, oblique, and converge ventrad. The clypeus is usually much wider than long and is divided usually into postclypeus (*po*) and preclypeus (*pe*) by a difference in color and by a transverse row of setae. Sometimes the clypeal suture (*cs*) is distinct, as in some *Nematinae* (Fig. 31). The clypeal setae vary in number from two to eight or ten but are constant within a genus and often within a subfamily. Four is the most common number.

*Labrum.*—The small lobe attached to the ventral margin of the clypeus is the labrum (*l*). It is usually transverse and has a median emargination on the ventral margin. This emargination is usually shallow and broad but occasionally very deep, as in *Eriocampa* and a few other *Emphytinae*. *Dolerus* (Fig. 42) is characterized by the distinct asymmetrical median emargination which makes the sinistral half of the labrum much smaller than the dextral. The cephalic margin is nearly smooth and slightly oblique in *Tremex* (Fig. 46). The labrum is very small in the *Xiphydriidae* (Fig. 45). From two to several labral setae (*ls*) are borne on each side of the meson, those near the meson being usually smaller than the lateral ones. The number of labral setae are as a rule constant within a genus. A row of setae which may be seen projecting from the ventral surface of the labrum belongs to the epipharynx. The labrum is often divided into halves by a distinct median longitudinal depression, as in *Caliroa* (Fig. 53), *Endelomyia* (Fig. 48), and some *Tenthredininae*. This character is generic in some subfamilies and only specific in others. The labrum in the *Cim-*



bicinae (Fig. 29) is unique in having a pair of longitudinal depressions on each half which converge ventrad and bound a small median piece.

*Postgenae*.—The area mesad of the lateral boundary of the vertex on the caudal aspect of the head is the postgena (*pa*). The dorsal boundary is the vertical furrow and the mesal the occipital foramen. The ventral margin is concave and is connected with the labicoria (*lc*). It is usually more or less flat and glabrous. The occipital suture (*os*) is sometimes distinct, as in *Pteronidea*.

*Tormae*.—At each end of the clypeo-labral suture there is a chitinized rod which extends onto the ventral surface as far as the epigusta. This is the torma, present in all *Tenthredinidae*.

*Occiput*.—The narrow area on the dorsal third of the occipital foramen between the vertical furrows is the occiput. The dorsal boundary is indistinct since the occiput merges with the vertex without any indication of a suture.

*Maxillariae*.—The very narrow chitinized sclerites which form a sub-circular collar around the dorsal and lateral margins of the occipital foramen have been identified as the maxillariae (*my*). They are usually only slightly developed and are continuous with the cervacoria. The identity of these sclerites with the maxillariae of generalized adult insects is uncertain, but they occupy the same position as the maxillariae and consequently are considered as homologous with them. The dorsal third of the maxillariae in the leaf-miners *Metallus* (Fig. 35), *Phlebotrophia* (Fig. 37) and *Fenusinae* (Fig. 34), are strongly chitinized, distinctly concave, trough-like, and produced entad. Along this ental margin a part of the muscles which control the movement of the head are attached.

*Occipital Foramen*.—The large opening in the caudal aspect of the head thru which the internal organs of the head are connected with those of the body is the occipital foramen (*of*). The ventral margin of the occipital foramen is membranous and connected directly with the labacoria and cervacoria (*cc*).

*Precoila*.—The strongly chitinized acetabulum located near the ventro-mesal angle of the vertex or the dorso-lateral angle of the clypeus is the precoila (*pr*). The preartus of the mandible (*py*) articulates at this point. The precoila is distinct in all *Tenthredinoidea*.

*Mandibularia*.—The small transverse whitish or light-colored area ventrad of the ventral margin of the head on the cephalo-lateral aspect is the mandibularia (*mb*). It is usually only slightly chitinized and merges with the mandacoria without any indication of a suture. The extensacuta (*ec*) of the extensatendon of the mandible is usually distinct. The mandibulariae are sometimes very large, as in the *Xyelidae* (Fig. 27).

*Postcoila*.—The cup-shaped acetabulum on the latero-ventral angle of the postgena and caudal angle of the mandibularia is the postcoila

(*ptl*), where the postartis of the mandible articulates. The occipital suture (*os*) when present originates in or near the postcoila. The postcoila is always present.

*Paracoila*.—There is a slight projection at the mesal end of the caudo-ventral margin of the head where the cardo of the maxilla articulates. This is the paracoila (*pl*). It is not well developed but is present and discernible in nearly all tenthredinid larvae.

*Odontoidea*.—The lateral cervical sclerite is articulated with the head capsule on the mesal margin of the postgena some distance ventrad of the origin of the vertical furrow. This point of articulation is an odontoidea (*od*) and is rather indistinct in the larvae of this group of insects.

*Tentorium*.—The tentorium is very simple in tenthredinid larvae. It consists of the metatentoria (*mt*), corpotentorium (*ct*), and pretentoria. The supratentoria are apparently obsolete. The metatentorium is the strongly chitinized conspicuous ental bar extending into the head capsule from the ventro-mesal margin of each postgena. The two metatentoria fuse on the meson and form the bridge, the corpotentorium, which gives support to the caudo-ventral portion of the head. The position of each metatentorina is indicated by a pit- or slit-like depression (*mn*). The location of the pretentorinae (*pn*) has already been indicated. A strong ental arm, much smaller than a metatentorium, extends ventro-mesad from each pretentoria into the head capsule and fuses with the corpotentorium near the middle of the latter. This bar is a pretentorium. In ecdysis the tentorium breaks in the middle of the corpotentorium, freeing the mesal ends of the pretentoria and metatentoria. The tentorium in the Xyelidae and Pamphiliidae is similar to that of the Tenthredinidae in structure and location.

The movable parts of the head include all the appendages, that is, the antennae, mandibles, maxillae, and labium.

*Antennae*.—The antennae are present in the larvae of all Tenthredinoidea, but their structure, size, position, and number of segments vary in the different families and subfamilies. Each is borne by a distinct antennaria (*ar*) which is located in the ventro-lateral portion of the vertex; in the generalized families they are located cephalad of the ocularia; in the specialized, ventrad of them. The antennariae are usually subcircular or subquadrate. The antacoria (*an*) is usually extensive, distinctly convex, and whitish in color (Figs. 143-153). It is only occasionally narrow and confined to the periphery of the antennaria, as in certain Nematinae (Fig. 154). The antennae of the Pamphiliidae (Fig. 26) are setiform, one-half as long as the head is wide, with seven cylindrical segments. There is a circular sensorium on the ventral aspect of the distal portion of the second, third, and fifth segments (Fig. 39). In the Xyelidae (Fig. 27) the segments are shorter but thicker, and vary in number from six to seven

according to the genus. The antennae of the Tenthredinidae (Figs. 145, 147, 149, 150, 153) apparently represent a specialization from those of the Xyelidae. They are much shorter and vary in number of segments from one to five. The antennae vary in shape and are conical in the Emphytinae and other generalized subfamilies, with five ring-like or limpet-shaped segments, with four more or less irregular, incomplete, often partly fused segments in the Nematinae (Fig. 145), or flattened and fused into a single segment in the Schizocerinae or button-like and one-segmented in the Cimbicinae, Fenusinae, and Metallus (Fig. 147), or subconical or irregular as in some Nematinae and Phlebatrophia (Fig. 150). When the antennae consist of five segments, they are usually cylindro-conical and remarkably uniform in shape. The antennal segments are usually strongly chitinized, more or less ring-like, successively smaller in diameter, and the distal segment is conical or occasionally erect and peg-like as in the Diprioninae. The segments do not always form a complete ring; one side may be reduced to a mere line, or be entirely wanting as in some Nematinae, in which cases the segment is said to be incomplete. Sometimes fusion of all or some of the segments may take place. Certain segments are sometimes setiferous and also bear some sensoria. The number of segments is constant for a subfamily. The relative length and shape of the segments vary, but are constant in species in some cases, and in others constant in genera. The antennae of the Cephidae are small, with four or five segments, while in the Xiphydriidae they are three-segmented and in the Siricidae and Oryssidae single-segmented. It is possible, therefore, to arrange the families of Tenthredinoidea in an ascending series according to the number and size of the segments of the antennae. The tenacity of the antennae is well illustrated in the Oryssidae, which in spite of the extreme modification of other structures still retains one-segmented antennae.

*Mouth-parts.*—The larvae of the Tenthredinoidea possess well-developed mandibulate mouth-parts. They include the mandibles, maxillae, and labium, and are remarkably uniform and constant in structure in the different families. The modifications take place in the relative size of parts and in the number of segments of the articulated parts.

*Mandibles.*—The mandibles (*md*) are always present, and are typically thick, strongly chitinized, and sharply dentate, the dextral dissimilar to the sinistral in the number and shape of the dentes, and in having one or two and occasionally more mandibular setae on the lateral aspect. The number and arrangement of the dentes, the number of mandibular setae, and the relative size and shape of the mandibles are constant for certain genera. The mandibles of the Schizocerinae are rather thin and flattened, and in Phlebatrophia very thin and elongated with one triangular blade-



like dentis. In this character the larvae of this genus are more specialized than all other larvae, even including *Oryssus*.

*Maxillae*.—The maxillae (*mx*) are always present and typically consist of cardo, stipes, subgalea, palpifer, palpus (*mp*), galea (*gl*), and lacinia (*la*). The cardo is usually more or less chitinized and is divided into a small subcardo and a larger triangular alacardo. The subcardo articulates with the head in the paracola. On the lateral margin of the alacardo the large stipes is attached. The stipes is usually less chitinized than the cardo, submembranous, convex on the lateral aspect, and attached to the lateral margin of the alacardo. The cephalic aspect is membranous and is continuous with the maxacoria. The caudal aspect along the mesal margin is strongly chitinized and continuous with the elongate triangular subgalea. The line of fusion is indicated by a distinct oblique chitinized ridge which extends from near the proximal end of the subgalea to the lateral angle of the lacinia. The latero-ventral angle of the stipes is often produced as a small triangular lobe, the stival angle of Crampton (1921) as in the Tenthredininae. The palpifer is a more or less membranous, mound-like lobe attached to the distal end of the cephalic margin of the stipes and often bears one or more setae. The palpus is borne by the palpifer and typically consists of four more or less conical segments. The relative size and shape of the segments vary and afford good characters for the separation of genera and species. The galea is typically strongly chitinized, digit-like, conical or slightly curved mesad, bluntly pointed, unsegmented, and usually smaller than the palpus. The lacinia is located mesad of the galea and cephalo-ventrad of the subgalea. It is usually subtriangular, slightly flattened, lobe-like, and bears a row of setae on its oblique mesal margin. It is sometimes distinctly flattened, strongly chitinized, with a stiff row of setae, as in the Emphytinae, or rounded and with minute spinous setae as in Diprion, or with a sharp triangular compressed seta in addition to an ordinary row of setae as in the Xyelidae. The galea and lacinia are always present except in *Oryssus* but are reduced in size in *Tremex*. It is interesting to note that in the leaf-miners the palpi are reduced but the galea are usually normal in size and larger than the palpi. In *Oryssus* the maxillae are fleshy lobes with all the component parts obsolete and with a brownish area in which a few sensory papillae are located (Rohwer and Cushman, 1917). The palpi are apparently two-segmented in the Xiphydriidae and Siricidae.

*Labium*.—The labium (*li*) consists typically of submentum, mentum, stipulae, palpiger, palpi (*lp*), and togaglossa—representing the fused glossae and paraglossae. The submentum (*sm*) and mentum (*m*) is typically membranous, convex, with two or more setae, and very broad in the larvae of most species. In some cases, as in the Diprioninae, part of the mentum is chitinized. In the leaf-miners, such as *Fenusa*, *Metallus*,



and Phlebotrophia, the mentum is strongly chitinized and flattened. There is a distinct median longitudinal depression in *Metallus*. The palpiger is practically wanting. The palpus is typically three-segmented (Fig. 157). The relative size and structure of the segments vary, but are usually constant for a subfamily or a genus. In *Tremex* and *Phlebotrophia* the palpi are apparently two-segmented and very minute, while in *Oryssus* they are obsolete. The stipulae are typically membranous, broad, sometimes bearing two setae, and fused with the mentum without any indication of a suture. The stipulae are flattened and chitinized in *Metallus* and the *Fenusinae*. *Totaglossa* is typically membranous, subglobose or bluntly pointed, fused with the stipulae without any indication of a suture. It is readily identified on account of its median position and characteristic shape and structure. There is a slit-like opening for the duct of the silk-gland, the sericos (*crv*) on the meson near the caudo-ventral aspect of the totaglossa. The shape, size, and location of the sericos vary but it is always present and chitinized. The cephalic or dorsal aspect of the totaglossa is strongly convex, membranous, and sometimes bears a few minute setae and sensoria.

*Prepharynx*.—The prepharynx, the so-called "hypopharynx" of the larvae of the Tenthredinoidea, is very simple in structure and the boundaries of the parts that can be identified in generalized insects (Yuasa, 1920) are obsolete. The propharynx consists of the epipharynx and epigusta. The epipharynx is membranous, is of the same size and shape as the labrum, and bears an oblique row of a few setae on each side slightly dorsad of the ventral margin. The epigusta is membranous and is supported on each lateral portion by a torus. The ambipharynx is restricted and membranous. The parapharynx consists of the basipharynx and hypopharynx (*hx*). The basipharynx is subglobose or convex, often slightly chitinized on the sides, sometimes having a few minute setae, and usually converges ventrad. The portion ventrad of the constriction is considered as belonging to the hypopharynx, but is usually membranous and continuous with the cephalic surface of the totaglossa without any indication of differentiation. The laciniae fit against the sides of the constricted part of the parapharynx. No striking modification in form of the prepharynx appears in the different families.

*Trunk*.—The portion of the body caudad of the head is the trunk. It consists of thirteen segments which connect with the head by means of the cervacoria. The first three segments compose the thorax and the remainder the abdomen.

*Cervacoria*.—The membrane (*cc*) which connects the thorax with the head is rather broad and usually folded under the protruding cephalic end of the prothorax. There is a chitinized sclerite on each side, the cephalic end of which articulates with the head against the odontoidea and the

caudal end with the epimeron and coxa. This is the lateral cervical sclerite (*lcs*), which is always present and usually distinctly colored—brownish or blackish. The cervacoria is continuous with the submentum on the ventral aspect, and is often produced on the meson as a small mound-like setiferous protuberance, as in *Strongylogaster*.

*Thorax*.—The prothorax is usually constricted on the cephalic portion, the dorsal aspect is declivous, and the lateral aspect is produced. The dorsum is typically divided into a narrow cephalic portion and a wide caudal one, which in turn may be subdivided into two or more annulets (Fig. 65). The first division is usually setiferous on the lateral aspect, while the second division is setiferous on the dorsal aspect. On the middle of the lateral aspect there is a large spiracle. This is the mesospiracle (*msh*), which has migrated onto the prothorax. There is another setiferous area cephalo-ventrad of the spiracle. The prothoracic leg is attached to the latero-ventral margin of the segment, ventrad of the setiferous subspiracular area, which is usually produced as a lobe and which Crampton (1918) has designated as the surcoxal plate. There is a small, usually strongly chitinized sclerite cephalad of the leg. This is the episternum-epimeron, or the eupleuron of Crampton. The dorsal aspect of the prothorax and often the lateral one may be chitinized and colored, forming shield-like areas as in the *Xyelidae* and certain leaf-miners. The prosternum is usually membranous, subdivided into two or more annulets, but sometimes it is flattened and strongly chitinized as in *Metallus*. There is usually a small pit or chitinized rod near the caudal part of the segment on the ventral aspect. This is the profurcellina (*pfn*) and marks the caudal limit of the prosternum. The mesothorax and metathorax are more or less similar in structure, frequently the largest segments in the body, more or less ring-like and often distinctly annulate. The metaspiracles (*tsh*) are located in the metacoria and are usually minute and functionless. The mesothorax and metathorax resemble the prothorax in other details. In the *Fenusinae* (Fig. 21) and *Metallus* (Fig. 22) the dorsum of the mesothorax and metathorax is provided with an ovoid, fleshy, sucker-like, low protuberance (*scp*) on each side of the meson. Its function is not known. *Dimorphopteryx* is characterized by the presence of a pair of prominent dorsal protuberances on the prothorax and a median protuberance on the mesothorax.

*Thoracic Legs*.—The larvae of the Tenthredinoidea, with the exception of the *Oryssidae*, possess three pairs of thoracic legs. They are the most persistent of all the thoracic and abdominal appendages and as a rule are very similar in structure, both facts indicating a common origin. A typical leg consists of five more or less well-chitinized segments: coxa, trochanter, femur, tibia, and a distal segment representing the fused tarsus and tarsal claw.

The coxa (*cx*) is usually the largest of all the segments, subconical, and articulated to the ventro-lateral margin of the segment. The cephalo-dorsal angle is strongly chitinized and articulates against the chitinized end of the episternum-epimeron. There is a distinct oblique depression extending from this angle to the middle of the dorso-distal margin of the coxa. The distal ends of the coxae are usually chitinized and form ring-like thickenings. The ventral half of the coxa is more or less membranous. The trochanter (*tr*) is usually small, longer on the ventral than on the dorsal aspect. The femur (*fm*) is usually cylindrical and is often dilated at the distal end. Its ventro-distal portion is usually membranous and is sometimes produced, forming a pointed projection, the femoral process (*fp*), as in *Dolerinae* (Fig. 135) and in related subfamilies. The tibia (*t*) is subcylindrical, narrower in diameter at the distal than at the proximal end, and either longer or shorter, than the femur or subequal to it. The distal segment is typically very short and claw-like. The apparent claw (*cw*) represents a fusion of the tarsus and tarsal claw, and is usually sharp and distinctly curved. The segments are usually setiferous and more or less membranous on the ventral aspect and at the joints.

The general plan of structure of the legs is the same in a majority of the larvae, but there are variations in the shape, size, arrangement of setae, and in the number of apparent segments within the families and subfamilies. The variations usually consist in the suppression of the trochanter as in *Phlebatrophia* (Fig. 136) and the *Fenusinae* (Fig. 140), or in the modification of the distal segment as in the *Pamphiliidae* (Fig. 130) and *Hylotominae*, or in the reduction of the entire structure to a fleshy, subconical, indistinctly segmented clawless protuberance as in *Phlebatrophia* and certain highly specialized families. The absolute homology of the segments in a modified leg can not be established, but when the number of the segments is less than five it is probable that the trochanter is the first one to disappear.

The *Pamphiliidae* are distinct from all other tenthredinoid larvae in having setaceous legs with all segments cylindrical except the distal ones. The distal segment is very slender, non-setiferous, straight, and sharply pointed without indication of a claw. The *Xyelidae* (Fig. 131) possess legs which are small but typical in structure and number of segments. It is quite possible to derive the normal tenthredinid legs from those of the *Xyelidae*. In the subfamilies of the *Tenthredinidae*, a series of modifications of the legs is found, altho the majority of the subfamilies and genera are provided with typical five-segmented, well-developed claw-bearing legs. The *Phyllotominae* (Figs. 141, 142) are characterized by very short, stubby, chitinized legs which consist of four segments, including the large strongly curved claw. *Phlebatrophia* (Fig. 136) is unique among the *Tenthredinidae* in having fleshy, rudimentary clawless legs. The *Fenusi-*



nae (Fig. 140) also possess small four-segmented legs but, unlike the Phyllostominae, have simple and ring-like segments and claws normal in form. The Hylotominae differ from the other subfamilies in possessing apparently six-segmented legs. Their distal portion consists of a distinctly separated tarsus and claw and bears an empodium-like fleshy lobe on the caudal portion of the claw. The minimum number of segments is found in the legs of the Schizocerinae (Fig. 139), where the mesothoracic and metathoracic legs consist of only three simple cylindrical segments, while the prothoracic legs are composed of four. There is a well-developed fleshy subglobose lobe caudad of the claw. It is interesting to note that the gall-makers, for example, *Pontania* have essentially the same type of legs as the leaf-feeding *Nematinae* (Fig. 133), while the leaf-mining larvae of the *Fenusinae*, *Schizocerinae*, and others, have modified legs. The highly specialized families, *Cephidae*, *Xiphydriidae*, and *Siricidae*, possess fleshy, indistinctly segmented rudimentary legs which are never provided with claws. The most specialized family, *Oryssidae*, is entirely apodous. The legs present, therefore, very good characters for differentiating the families and the subfamilies of the Tenthredinoidea. The phylogenetic significance of the thoracic legs is quite evident.

*Abdomen.*—The segments composing the abdomen, with the exception of the two caudal segments, are more or less similar in structure, ring-like, and usually subdivided into four to seven annulets. Segments 2-7 or 2-8 and 10 usually bear a pair of larvapods, the so-called "prolegs," on the ventral aspect. The first and ninth abdominal segments never possess larvapods except in the *Xyelidae*. The third abdominal segment is more typical than the other segments and least modified, and for this reason has been used as a type for description. In a typical larva this segment is subdivided into a number of annulets on the dorsum and *latus dorsad* of the spiracular line. The *latus ventrad* of the spiracular line is typically lobe-like, setiferous, and distinguishable as two areas, the subspiracular area (*ssl*) or the surpedal area (*sdl*) according to the location. When these areas are distinctly lobe-like they are designated as subspiracular lobe and surpedal lobe. The latter corresponds to the thoracic surcoxal plate of Crampton. The subspiracular and surpedal lobes sometimes fuse and extend the full length of the segment as an oblique fold, as in wood-boring larvae and the *Hylotominae*. In the latter this lobe is conspicuously produced laterad, making the segment distinctly flattened. The subspiracular and surpedal lobes, when fused, are known as the sublateral lobe (*sl*). The larvapods are located on the ventral aspect some distance from the meson. The sternum is divided into two or more annulets, the annulation being usually distinct but its exact limits difficult to determine on account of the presence of the larvapods. The intersegmental coria (*cor*) is distinctly indicated on the venter (Fig. 81). The segmentation



is distinct but the limits of the somites are not so readily determined. The cephalic limit of a segment is usually indicated by the distinct depression on the dorsal and lateral aspects and by the short ventro-lateral depressions which terminates at the cephalic end of the subspiracular lobe. Thus the cephalic limit of a segment is not a straight line, but curves caudo-ventrad and then slightly cephalo-ventrad of the subspiracular lobe. The typical annulation and arrangement of setae, tubercles, and glandubae on the typical abdominal segment are indicated elsewhere (Figs. 73-79). The ninth abdominal segment is readily distinguishable because of its location and shape, and by the absence of spiracles and larvapods. It is typically smaller than the preceding segments, tapers more or less caudad, and usually has one less annulet on the dorsum than have the preceding segments. Its caudal limit is usually distinctly indicated by a deep depression. The tenth, or the apparent ultimate, segment is modified and differs from the other abdominal segments because of the presence of the anus, anal larvapods, and other structures peculiar to this segment (Figs. 89-103).

*Tenth Urotergum*.—The tergum of the tenth abdominal segment is usually convex and often setiferous. It sometimes bears numerous spinous processes, as in the Blennocampinae and Dimorphopteryx, or paired suranal protuberances as in certain genera of Nematinae, or a median suranal process (*srp*), as in the Cephidae and its allies. In these highly specialized families the tenth abdominal segment is produced cephalad and fits into the deep semicircular emargination of the ninth segment. The tergum possesses a distinct, deep, median longitudinal depression extending from the cephalic end of the tergum to the proximal end of the median suranal process. In the Xyelidae the tergum is produced distinctly hunch-like on the meson of the cephalic third caudad of the deep, broad transverse depression. The tergum is produced caudad in certain species of Pachynematus and forms a distinct caudal projection. In this genus the glandubae are very conspicuous. The size, convexity, number, and arrangement of the spinous protuberances, caudal processes, and setae are useful characters in recognizing different subfamilies and genera.

*Suranal Lobe*.—The membranous lobe (*srl*) of the Tenthredinidae, which forms the dorsal wall of the anal slit may represent the rudiment of the dorsal half of the ultimate segment, the so-called "telson." It bears numerous setae of varying size and number and is usually fused with the tergum of the tenth segment. In the larvae of the Xiphydriidae and its allies, which possess a median suranal process, the suranal lobe is distinct, more or less chitinized in part, usually separated from the tenth tergum by a ridge or by an oblique suture which extends from the chitinized depression dorsad of the suranal process to the lateral end of the anal slit (*au*). The area cephalad of this oblique suture is the pleuron of the tenth segment.

*Subanal Lobe.*—The membranous lobe (*sbl*) which forms the ventral wall of the anal slit may represent the rudiment of the ventral half of the ultimate segment or "telson." It is never distinctly chitinized, always indistinguishably fused with the tenth abdominal sternum, usually setiferous, and is rather restricted in extent. In the Tenthredinidae the subanal lobe is strongly convex and extends to the anal larvapods, the postpedes of Crampton. If the subanal lobe represents a part of the telson, and if the subanal appendages (*sba*) of the Pamphiliidae and Cephidae are the appendages of the ultimate segment, then the subanal lobe possesses a pair of genuine appendages. In the larvae of the Xyelidae there occur sometimes distinct subglobose setiferous swellings dorso-caudad of the anal larvapods. Their homology and function are unknown.

*Tenth Urosternum.*—The sternum of the tenth abdominal segment is restricted in extent, more or less convex, and often glabrous. In the Xyelidae and Tenthredinidae the anal larvapods occupy the greater part of the caudal portion, which is thereby produced subconically ventrad. This sternum is usually glabrous and more or less flattened in apodous larvae. There are no annulations observable on this sternum.

*Suranal Process.*—In boring larvae, the ultimate segment is provided with a strongly chitinized mesal suranal process (*srp*) on the suranal lobe. This process, which has been variously designated by different writers, is characteristic of the families Cephidae (Figs. 108, 109, 112, 114, 115) Xiphydriidae (Figs. 107, 110), and Siricidae (Figs. 113, 120, 122). The size, shape, number, and arrangement of the dentiform tubercles and setae vary in different families but they are constant within species and often also within genera. It is undoubtedly an adaptive structure developed in connection with the boring habit of the larvae. It is interesting to note that in some of the gall-making larvae of *Pontania* and leaf-stem boring larvae of *Caulocampus*, the tergum of the ultimate segment is produced on the caudo-meson and forms a distinct protuberance provided with chitinized points on its caudal end. The larvae of the Pamphiliidae also possess a minute hook-like process on the caudo-meson of the ultimate tergum. The genetic connection of this hook-like tubercle and the distinct suranal process of highly specialized families is doubtful, but it is not difficult to surmise a common origin for the suranal process of the Cephidae, Xiphydriidae, and Siricidae. The suranal process corresponds to the postcornu of Crampton.

*Caudal Protuberances.*—In certain genera of the Nematinae and in a few other genera of the Tenthredinidae, the tergum of the ultimate segment is provided with two or more protuberances which vary in size, shape, number, and position in different genera. A typical condition in nematid larvae is found in *Pteronidea* (Figs. 126, 127), which possess a pair of conical, pointed, well-chintinized processes (*srp*), one on each side,

on the caudal margin of the tergum dorsad of the membranous suranal lobe. These processes are always two in number and more or less constant in position in nematid larvae, but vary in size and shape altho constant within species. They are conical, subconical, sharply or bluntly pointed, truncate, or distinctly swollen at the distal end as in *Pteronidea trilineata*. The tenth abdominal tergum of the spinous larvae of the Blennocampinae is provided with several symmetrically arranged conspicuous spinous processes on the caudal portion and in part along the caudal margin. The larva of *Dimorphopteryx* is unique among the Emphytinae in the possession of four very distinct, sharply pointed spinous protuberances along the caudal margin of the ultimate segment dorsad of the suranal lobe. In certain of the gall-making species of *Pontania* the caudal end of the tenth abdominal tergum is produced caudad and forms a median prominence which usually has two minute strongly chitinized points close together on the meson. A similar protuberance is found in the larvae of *Caulocampus acericaulis*. In the Siricidae a pair of minute sharply pointed solid chitinized spines occurs on the tergum of the ultimate segment, one on each side of the median longitudinal depression (Fig. 113).

These protuberances have been variously designated. Crampton (1919) considers the paired protuberances and spines to be homologous with the cerci of Orthoptera and Ephemeridae. If they represent rudimentary cerci they must belong to the eleventh abdominal segment, the telson of embryologists, since the true appendages of the tenth segment are transformed into the anal larvapods. But this homology is open to question because these protuberances are mere projections of the surface and not at all appendages in a morphological sense, and, furthermore, because in other larvae the number and position of the protuberances vary considerably. No one would suggest that the caudal tubercles and spinous processes of *Dimorphopteryx*, *Blennocampa*, *Hypergyricus*, *Caulocampus*, and others are homologous with the cerci of generalized insects; yet, there is no reason to assume that the caudal tubercles of these larvae are different in origin, structure, and function—whatever that may be—from the suranal paired processes of the nematid larvae. These protuberances may or may not be at all related genetically to the suranal median process of the Cephidae and its allies. At any rate our present knowledge does not permit any definite conclusion regarding the true nature or homology of these structures. The interpretation advanced by Middleton (1921) seems more reasonable. He named these protuberances pseudocerci.

*Subanal Appendages.*—The larvae of the Pamphiliidae (Figs. 91, 95) and Cephidae (Figs. 108, 109, 111, 116, 117, 118, 119) possess a pair of subanal appendages on the ultimate segment, one on each side ventrad of the lateral ends of the anal slit. These appendages are long, setaceous, and three-segmented in the Pamphiliidae, but are rudimentary, papilliform,



and only indistinctly segmented in the Cephidae. When the appendages are long and setiform, the relative length and color of the segments differ in different species. In the Cephidae the appendages may or may not be provided with accompanying setae near the proximal end, and these setae may or may not form a continuous group with the setae on the sternum.

That these structures are true appendages of the segment is indicated by the segmentation and by the fact that they are invariably articulated at the proximal end against the surface, not being mere protuberances like the caudal processes of the tergum. Some embryologists consider these appendages to be homologous with the cerci of generalized insects and the anal "prolegs" of lepidopterous larvae, and, therefore believe them to be true appendages of the eleventh abdominal segment. It is obvious that they can not be homologous with the anal larvapods of other tenthredinoid larvae. Crampton (1919) designated them as arthrostyli on the ground that they are apparently homologous with the styli of the Ephemeridae and other insects. The opinions of entomologists differ, for example Middleton (1921) homologizes the subanal appendages with the postpedes of Crampton. The homology and function of these appendages need further investigation. However, it is significant that long distinctly segmented appendages should occur in the Pamphiliidae and rudimentary ones in the Cephidae.

*Larvapods.*—The embryological data seem on the whole to support the view expressed by Korschelt and Heider (1899), who say that "the abdominal appendages of the caterpillars of the Lepidoptera and Hymenoptera are to be regarded as true limbs," and that "limb-rudiments first form on all or most of the abdominal segments, but they very soon disappear on those segments which in the larvae have no limbs, while on the other segments they are transformed into the functional prolegs." Graber (1890) has shown that the so-called anal prolegs of *Hylotoma* are the appendages belonging to the tenth or true penultimate abdominal segment. They are, therefore, not homologous with the anal "prolegs" of lepidopterous larvae, which are, according to Graber (1890), the appendages of the ultimate segment.

The maximum number of larvapods (*plg*) occurs in the Xyelidae, where each of the abdominal segments is provided with a pair. The first and ninth pairs may be smaller than the others, as in *Odontophyes*, but they are always discernible. The number of larvapods present in the Tenthredinidae varies from six to eight pairs. They are usually present on abdominal segments 2-7 and 10 or 2-8 and 10, rarely on 2-6 and 10. In the *Fenusinae* (Fig. 105) and *Caulocampus* the tenth pair is obsolete, and in *Metallus* (Fig. 103) they are fused together forming a median protuberance. Larvapods are entirely wanting in the other families of the Tenthredinoidea.



A typical larvopod is a fleshy subconical protuberance narrowed toward the distal end, and is usually subdivided into a larger but shorter proximal portion and a smaller but longer distal portion. Sometimes the distal end is dilated and turned mesad, as in *Neodiprion* (Fig. 82), or the cephalo-ventral angle is pointed, as in *Tenthredo*. The larvopods are well developed in most of the free-living larvae but in the leaf-miners and fruit-borers they are reduced and smaller. They are very small in the *Hylotominae* and rudimentary in the *Fenusinae* (Fig. 86) and *Schizocerinae*, while they are obsolete in *Phlebotrophia*. The degree of development of the larvopods is closely correlated with the habits of the larva. The larvopods are usually located on the middle of each lateral half of the sternum but occasionally are very close together near the meson, as in *Neodiprion*. The number of pairs of larvopods present is a convenient character for differentiating the subfamilies of the *Tenthredinidae*. The larvopods often bear a few setae on the cephalic and lateral aspects. The setae, when present, are confined to the mesal aspect. Lack of setae on the larvopods is often a generic character and the number and arrangement of the setae is typical of the species.

Crampton (1919), with good reasons, proposed to substitute the term uropods for the long-used but misleading term prolegs. The term uropoda has been employed by students of the Crustacea in designating the abdominal appendages, especially one of the posterior pairs of pleopods, and according to Smith's glossary of Entomology the term refers to "any of the abdominal feet of Arthropoda." These facts indicate the necessity of a distinctive term, and the new term larvopods following the suggestion of Dr. MacGillivray, is used until a happier term is created for these true abdominal appendages of insect larvae.

*Metamerism*.—Graber (1890) has shown that the number of somites which compose the body of the larvae of *Hylotoma* is fourteen exclusive of the head. The first three somites belong to the thorax and the remaining eleven to the abdomen. The ultimate segment, or the telson of the embryologists, is difficult to discern in larvae. It is probably represented by the suranal and subanal lobes of the larvae, but the boundary between this segment and the tenth somite is so obliterated, and the ultimate segment, which is originally much smaller than the preceding somites, is in the larval stage so much more reduced, that it is permissible and also convenient to speak of the abdomen as being composed of ten segments. For this reason the tenth abdominal somite, which bears the so-called anal prolegs, is designated as the ultimate segment in this paper. It is to be noted that Nelson (1915:111) considers that there are eleven segments and a telson in the abdomen of the embryos of Hymenoptera. In all the larvae of the *Tenthredinoidea* examined, it is always possible to count ten abdominal segments. The body is usually distinctly segmented.

The exact limit of the somite in a larva is not easy to determine. Entomologists seem to have paid little or no attention to this point. Castle (1900) has made an excellent study of the metamerism of the Hirudinea, but his conclusions are not directly applicable to the case of insect larvae tho they are pregnant with important suggestions. He found that the natural and true limits of a somite coincide with the limits of the neuromere, and that both reduction and increase in the number of rings, which correspond to the annulets in the saw-fly larvae, take place at the ends of the segment. The classical work of Lyonet (1762) and the recent study of Forbes (1914) on the musculature of lepidopterous larvae, as also a study of Boving (1914) indicate that the musculature affords a reliable criterion for determining the limits of a somite. From a careful examination of the musculature of various types of tenthredinoid larvae (Fig. 129), the author has come to the conclusion that in these larvae the natural and accurate determination of the extent of the somites composing the body is best based upon the musculature. A detailed discussion of this subject is out of place here. It is sufficient to say that a majority of the longitudinal muscles, including the dorsal, lateral, and ventral retractor muscles, originate on the cuticular fold, or coria, which, on the exterior, is usually indicated by a deep depression (*is*). Only a few muscles of importance cross this fold, nearly all the muscles being attached either to the cephalic or caudal part of the coria. This cuticular fold, therefore, is considered as the cephalic limit of the somite, and the annulets into which the somite is subdivided are numbered consecutively, commencing at its cephalic end. To assume, *a priori*, the spiracular annulet, or the annulet which bears the spiracle, to be the first annulet is arbitrary and inaccurate inasmuch as this annulet, according to the criterion of musculature, corresponds to any one of the first three annulets of the somite. The position of the spiracular annulet is constant and definite within a genus or subfamily as long as the number of annulets of the somite is constant. Some of the annulets are usually setiferous and often bear in addition transverse rows of glandulae. The position of such setiferous annulets is constant within the genus or subfamily when the annulation is constant. The number of annulets on the ninth abdominal segment is always smaller than that on the preceding segments. Since the setiferous annulets have a definite order, it is possible to determine which annulets are obsolete on the penultimate segment. The first annulet to disappear is a caudal one, and ordinarily it is only the caudal annulet that is missing. The number of annulets of the sternum is less than that of the tergum. The length of the annulets varies but their relative size is constant within a species. The primitive number of annulets of the abdominal segments is unknown. If the annulation of the generalized Tenthredinoidea is assumed to be representative of the primitive condition, then four is the primitive num-

ber of annulets. In the specialized Tenthredinoidea the number varies from one to seven, but five to seven is of the most common occurrence. The number becomes smaller in the highly specialized families, being reduced to a single annulet in the Siricidae and Orysiidae.

*Spiracles.*—The spiracles (*spi*) are present on the prothorax and the first eight abdominal segments in all Tenthredinoidea. The pair on the prothorax are always the largest. The abdominal spiracles are usually uniform in size and shape except the last pair, which are often larger than the others. The spiracles are definite in location in regard to the annulets and are always situated on some one of the first three annulets of the segments. The spiracular line is usually located slightly ventrad of the middle of the lateral aspect of the body, but sometimes it migrates ventrad to the latero-ventral line as in *Caliroa*. The spiracles (Fig. 155) are usually very simple in structure, vertical in position, never circular in outline but narrowly ovate, rounded or pointed at both ends. The peritreme is narrow but strongly chitinized and brownish or blackish. The labiae are narrow and the spiracular opening is usually closed and appears like a dark line. The peritreme is sometimes distinctly thickened as in the Hylotominae. There is often a semicircular or irregular chitinized colored area on each side of the spiracles, as in certain nematid genera. These areas vary in size and shape but are constant within species, and their presence is usually constant within genera and often within a subfamily. When these areas are present, the spiracles are said to be winged.

The true prothoracic spiracles are considered as wanting in adult and larval insects. The spiracles found on the prothorax of Tenthredinoid larvae are the mesothoracic spiracles (*m<sub>sp</sub>*) which have migrated from the mesocoria onto the prothorax. The metathoracic pair (*t<sub>sp</sub>*) is usually functionless, very small, and located in the metacoria, or obsolete. In the Cephidae and Siricidae, however, the metaspiracles are distinct, functional, and as large as the abdominal spiracles. It is difficult to explain the rudimentary condition of this pair in the Xiphydriidae, since other characters indicate that they have a common origin with the Cephidae and Siricidae. It is possible, however, in the course of evolution, to have one structure of the body modified faster than another structure.

*Setae.*—The surface of the body is usually provided with some setae, particularly on the head, thoracic legs, and the ultimate segment of the abdomen on the suranal and subanal lobes. The number, size, arrangement, and structure of the setae vary in different taxonomic units, according to their location; and to some extent according to the stage of larval growth. There is a tendency toward the loss of setae in the ultimate stage or the last instar, as is Pteronidea, or to have fewer and smaller setae in the leaf-mining and wood-boring larvae, as in the Fenusinae, Cephidae, and others. There seem to be no definite setal patters, as in lepidopterous



larvae, but when certain annulets of the segments possess setae their presence on these annulets in successive segments is constant if not in precisely the same number and order. There is a tendency to have more and longer setae on the lower half of the head than on the upper half. The number and arrangement of the setae are variable on the vertex and front but are fairly constant on the clypeus, labrum, and mandibles.

A spinal formula is an abbreviated expression of the arrangement of the tubercles or spines on the various parts of the body. The figures of the formula indicate the number of branches of a spine and are arranged in order, beginning with the mesal spine in the case of those on an annulet and with the cephalic spine in the case of the subspiracular areas. The spinal formula of the prothoracic segment represents the arrangement of the spines on the large or second annulet, on the first or smaller lateral annulet, on the subspiracular area, and on the postsubspiracular area respectively. The spinal formula of the third abdominal segment indicates the arrangement of the spines on the first tubercle-bearing (usually 2d) annulet, on the next small annulet if this is present, on the third tubercle-bearing (usually 4th) annulet, on the subspiracular area, and on the postsubspiracular or surpedal area, respectively.

The number of branches of the spines sometimes varies and the arrangement of the spines also may show minor variations. The spinal formulae represent the most typical arrangement.

*Glands and Glandubae.*—There are many types of glands opening to the exterior found on the various parts of the body of the larvae of the Tenthredinoidea. The larvae of the Nematinae and Cladiinae are provided with a series of ventral glands on the ventro-meson of abdominal segments 1-7. Sometimes a pair of eversible glands is found in the cervical region, as in *Megaxyela major*. The larvae of the Cimbicinae possess a spiracular gland located dorsad of each spiracle of abdominal segments 2-8. It is from these glands that the yellowish fluid of these larvae is poured out when disturbed. A peculiar sucker-like protuberance with a depressed center occurs in the larvae of the Acordulecerinae on the sublateral area of abdominal segments 2-4 or 5 and 8. The function of this structure is not known but it is not improbable that it is secretory in nature. The wax glands of the wax-secreting larvae such as certain Tenthredininae, Emphytinae, Selandriinae, etc., are minute and located on various parts of the body of these larvae, but their detailed structure has not been studied. The most common type of these glands is found in the larvae of the Diprioninae, Emphytinae, Selandriinae, Tenthredininae, some Nematinae, and others. The cutaneous glands of these larvae are provided with chitinized rings about their external openings. These chitinized openings are known as glandubae. They may be located at the end of tubular protuberances, and in such cases they are spoken of as being stalked, or they



may be found flush with the body surface, when they are spoken of as being sessile. The glandubae are especially conspicuous in the larvae of the Diprioninae and Pachynematus. The slime-glands of Caliroa have semi-sessile glandubae which are few in number. The glandubae are constant in their type, presence, general arrangement, and location, within genera and subfamilies.

*Formulae of Segmented Appendages.*—For convenience in designating the size and relationship of various segmented appendages, the resort has been made to various so-called formulae. The segments of an appendage are numbered, beginning with the proximal segment. In a formula numbers of the segments are arranged in the descending order of magnitude, and those of equal dimensions are placed in a parenthesis. For example, the expression “antennal formula: (2,5), 3, 4, 1” shows that the antenna is composed of five segments and that segments 2 and 5 are equal in length but longer than the others, and that segment 4 is shorter than segment 3 but longer than the first or proximal segment.

### III. TAXONOMY

Strictly speaking no classification of the Tenthredinoidea based upon larval characters has hitherto been proposed. Attempts have been restricted to the characterization of the different subdivisions included in the superfamily. Among the earlier writers Le Peletier's (1823) work may be mentioned. After a brief general account of the larvae, he gave a list of eighteen divisions in which he grouped the species of the Tenthredinoidea and stated whether the larvae of each division were known or unknown and, if known, the number of the thoracic and abdominal legs present. It is interesting to note that he mentioned a group of larvae the body of which he characterized as "donkey-form" (aselliform) which he was unable to place in any of his divisions. Dahlbom (1835) published careful descriptions and a synopsis of larvae of sixty-three species. A synoptic table for the larvae was compiled by Westwood (1840) from this work and was published with additions. The characters used are the number of abdominal legs and the feeding habits of the larvae. Norton (1867) republished Westwood's table without additions. In the table given by Cameron (1882) the larvae of more than ninety-five species are included. The major groups are separated on the number of thoracic and abdominal legs present. These subdivisions are segregated on biological characters such as reflex bleeding, types of cocoons, and, finally, genera and species, when known, are separated on the coloration, setae, food-plants, and feeding habits. In 1895 Dyar, the most prolific and the only important American writer on the larvae of the Tenthredinoidea, published "A recognition table for the known sawfly larvae of the North Atlantic States." The larvae of one hundred and twenty-six species including forty-one not specifically identified were considered in this synopsis. The characters used are the number and location of abdominal legs, types of cocoon, feeding habits, food-plants, and coloration. This last character was employed extensively in separating different species. The next attempt along this line was undertaken by Chester Young (1898), who was the first to take into consideration the structural characters of the appendages of the head. Unfortunately this work remains unpublished, but it is on file as a baccalaureate thesis in the library of Cornell University. Konow (1901) summarized the taxonomic information concerning the known larvae of European and American species, four hundred and eighteen in all, in the form of an analytical table. The presence or absence of abdominal legs, number of antennal segments, and modifications and appendages

of the ultimate body-segment were used in separating the families and subfamilies. The number and location of abdominal legs, the food-plants, types of cocoon, and coloration furnished the basis for the separation of tribes, genera, and species. Middleton (1915, 1917) has characterized the larvae of the genus *Dimorphopteryx* and of the family Cephidae. It must be noted that these writers were concerned only in the preparation of recognition tables for the separation of the particular species they had in hand, and, with the exception of Middleton, no one has attempted to construct a synopsis of families, genera, and species as such.

In the following pages, the author has attempted to define and describe, as far as possible with the materials at hand, families, subfamilies, genera, and species by the use of larval characters. With a few exceptions, no attempt has been made to incorporate data from previous writers for the reason that the characters recorded by them were found in most cases of little or no value for the present purpose—not because they were inaccurate, altho that was true in many cases, but chiefly because they were not of specific significance. For example, Dyar's descriptions of species are usually very accurate and dependable but most of the characters noted excepting coloration often proved to be only of family or subfamily significance. The definitions given here are correct for the materials actually studied, but it is not surprising if they do not hold good in many cases when more materials become available for examination. It is obviously impossible to attain perfection in the face of so many missing links in the series of genera and species. These missing links will be filled in as rapidly as accurately identified materials become available, but it must be remembered that absolutely correct identification is only possible, in the majority of cases, after carrying individual larvae of the species thru to the adult stage, exuviae being saved for each instar.

In this study the classification of the Tenthredinoidea proposed by MacGillivray in 1906, with later additions, has been adopted in the main in arranging and restricting the families, subfamilies, genera, and species. For generic synonymy, Rohwer's "Genotype of the Sawflies and Woodwasps" (1911) has been followed. In this section all references to the bibliography of the different divisions and subdivisions have been omitted.

## SUPERFAMILY TENTHREDINOIDEA

Larvae with exposed, well differentiated head, trunk consisting of three thoracic and ten visible abdominal segments; spiracles always present on prothorax and first eight abdominal segments; antennae and chitinated dentate mandibles always present; ocellaræ, when present, always one on each side of the head; thoracic legs, when present, always three pairs, a pair to each segment; larvapods, when present, always six pairs or more, and except the Xyelidae, are never on the first and ninth abdominal segments, but always on the second abdominal segment, and never with crochets; mouth-parts, when normal, with mandibles strongly chitinated with distinct dentes, dextral dentes differing in number, shape, and arrangement from sinistral; maxillæ with cardo, stipes, palpifer, palpus, galea, and lacinia present, palpus typically with four segments, galea conical, digit-like, and lacinia usually flattened, its cephalic margin with a fringe of setae; labium with submentum, mentum, palpi, stipulae, and totaglossa, palpi typically with three segments, totaglossa membranous, bulbous, with a sericos on its meso-distal portion; general appearance of body caterpillar-like or grub-like; free leaf-feeders, leaf-miners, web-spinners, leaf-rollers, wood- and stem-borers, and parasitic larvae.

*Free Leaf-feeders.*—Body caterpillar-like; thorax with well-developed, distinctly segmented legs, typically with five segments, coxa, trochanter, femur, tibia, and tarsus and tarsal claw; abdomen typically with a pair of larvapods on segments 2-7 or 2-8 and 10; ultimate segment sometimes with caudal protuberances but never with a distinct suranal process or with subanal appendages; head typically semiglobose; antennae typically multisegmented, segments one to five in number; ocellaræ always present, usually located dorsad of antennariae; mouth-parts well developed and typical in structure; abdominal segments usually with five to seven annulets, some of which bear transverse rows of setae and often some glandubae; head, thoracic legs, and anal area usually setiferous; majority of Tenthredinidae and Xyelidae.

*Leaf-miners.*—Body somewhat depressed, head sometimes distinctly depressed and mouth-parts directed cephalo-ventrad; thoracic legs small, modified, number of segments reduced to four or to one, legs sometimes entirely fleshy, conical, or mamma-like, with or without tarsal claws; abdomen with very small larvapods or larvapods nearly obsolete; mouth-parts sometimes modified, labial and maxillary palpi with reduced number



of segments; annulation sometimes obsolete. A few subfamilies of Tenthredinidae.

*Nest-builders*.—Thorax with seta-like segmented legs; abdomen without larvapods; antennae long, setaceous, seven-segmented; mouth-parts normal; ultimate segment with distinct subanal appendages and a minute hook-like caudal process on caudo-meson of tergum; ocellaræ present; web-spinning leaf-rollers, Pamphiliidae.

*Borers*.—Thorax with rudimentary legs, tarsal claws never present; abdomen without larvapods, ultimate segment with a distinct suranal process or with a pair of subanal appendages; mouth-parts somewhat modified, maxillary and labial palpi reduced in number of segments; ocellaræ wanting or with vestigial eye-spots; metaspiracles sometimes functional, as large as abdominal ones; wood-borers and stem-borers, Siricidae, Xiphydriidae, and Cephidae.

*Parasites*.—Body grub-like, thoracic and abdominal legs wanting; mouth-parts modified, maxillary and labial palpi obsolete; ocellaræ wanting; antennae one-segmented; parasitic larvae, Oryssidae.

The larvae of the typical Tenthredinoidea are readily differentiated from the larvae of other Entometabola by the presence of a single ocellara on each side of the head and, usually, six or more pairs of larvapods, none of which are provided with crotchets, and never occur on first and ninth abdominal segments. The characteristic mouth-parts include four-segmented maxillary palpi and three-segmented labial palpi. The character of the antennae, the number of ocellaræ and larvapods, the character of the mouth-parts, especially maxillary and labial palpi, and the presence of thoracic legs distinguish the leaf-miners and wood-borers of the Tenthredinoidea from other leaf-miners and wood-borers, such as certain Lepidoptera, Coleoptera, and Diptera. The larvae of Hymenoptera other than Tenthredinoidea are distinguishable from those of the latter as follows: They are apodous, thoracic and abdominal legs being always wanting; the mouth-parts are vestigial, maxillary and labial palpi, if present, papilliform, never distinctly segmented; ocellaræ are never present; and suranal process and subanal appendages are always wanting. The larvae of the Oryssidae are separable from other hymenopterous larvae on the basis of the characters used in the definition of that family elsewhere.

#### FAMILIES OF TENTHREDINOIDEA

- 1(6) Thoracic legs present, either normal in form, distinctly segmented, or modified, if modified, fleshy or conical, if conical, head and body distinctly depressed; larvapods either present or wanting.....2.
- 2(5) Thoracic legs normal in form, not seta-like, rarely mamma-like; larvapods usually present; subanal appendages wanting; antennae usually with less than seven segments.....3.

- 3(4) Larvapods present on all abdominal segments; antennae with six or seven segments.  
XYELIDAE.
- 4(3) Larvapods not present on all abdominal segments; antennae never with more than five segments.....TENTHREDINIDAE.
- 5(2) Thoracic legs seta-like; larvapods wanting; subanal appendages present, setaceous; antennae very long, with seven segments.....PAMPHILIIDAE.
- 6(1) Thoracic legs vestigial, not distinctly segmented, mamma-like or wanting, if mamma-like, head and body never distinctly depressed; larvapods wanting.....7.
- 7(12) Thoracic legs present; ultimate segment with suranal process.....8.
- 8(9) Subanal appendages present, vestigial, papilliform; ocellaræ present; antennae with four or five segments.....CEPHIDAE.
- 9(8) Subanal appendages wanting; ocellaræ wanting.....10.
- 10(11) Antennae with three segments; metaspiracles functionless, very much smaller than abdominal spiracles.....11.  
XIPHYDRIIDAE.
- 11(10) Antennae with one segment; metaspiracles functional, as large as abdominal spiracles.....SIRICIDAE.
- 12(7) Thoracic legs wanting; ultimate segment without suranal process and subanal appendages.....ORYSSIDAE.

MacGillivray (1906) divided the superfamily Tenthredinoidea into nine families. They are the Xyelidae, Pamphiliidae, Blasticotomidae, Tenthredinidae, Xiphydriidae, Siricidae, Megalodontidae, Cephidae, and Oryssidae. The first two families constitute his Generalized Tenthredinoidea and the last six his Specialized Tenthredinoidea. Since the Blasticotomidae and Megalodontidae belong to the Palearctic fauna and are not represented in North America, they are omitted from the foregoing table.

#### FAMILY XYELIDAE

Larvae (Fig. 6) of medium size, length 13-18 mm.; body caterpillar-like, subcylindrical, flattened on the ventral aspect, uniform in diameter except last two segments which are suddenly constricted, stout; segmentation and usually annulation distinct; cuticle smooth, tuberculate and setiferous, but never slimy; color greenish, yellowish, whitish, or brownish; tubercles, when present, brownish or blackish and setiferous; prothorax sometimes with a pair of lateral eversible cervical glands in the cervacoria; head circular in frontal contour, moderately large, width usually more than one-half the diameter of the thorax; mouth directed ventrad; head slightly overlapped by the prothorax, if any setae, sparsely and inconspicuously setiferous; antennae long, conspicuous, with six, sometimes seven, segments; ocellaræ about one-fifth the diameter of the antennaria and located caudo-dorsad of it, elevated, ocellaræ very small; epicranial suture and vertical furrows present; mouth-parts normal in form; prothorax with a large, often colored, shield-like area on the dorsum and lateral aspects; legs in comparison with the size of the body very small, normal in form, all three pairs subequal in size; larvapods present on all

abdominal segments including the first and ninth, where they are sometimes reduced in size; typical segments with four annulets; spiracles on the second annulet; sublateral lobe produced ventrad, modified into a triangular lobe laterad of larvapod which it resembles in form; ninth abdominal tergum with three annulets; tenth abdominal tergum constricted distinctly and transversely on its cephalic fourth and with a distinct hump-like protuberance on the meson caudad of the cephalic constriction, concolorous with the head and setiferous tubercles; anal larvapods and ventral or subanal lobes distinctly large, contiguous, forming a trilobate prominence on the meson of the tenth sternum; subanal lobe with a pair of setiferous protuberances dorsad of larvapods; insects single-brooded, solitary, chiefly exposed-feeders; pupate in earthen cells in the ground.

The Xyelidae is a small family consisting of seven genera and of a limited number of species, most of which belong to the North American fauna. The adults are readily distinguished from all other Hymenoptera by the presence of the free part of the vein  $R_2$  in the wings. On venational characters, MacGillivray (1906) considers the members of this family to be the most generalized Hymenoptera known, having, "departed from the type of the wing assumed for the original progenitor of the Hymenoptera only in the loss of the free part of vein  $Cu_2$ ." The genera, at the same time, possess many features of prominent progressive specializations which have proceeded in each case in a different sequence so that a linear arrangement of the genera does not express their true affinities.

Over twenty-five species have been reported from boreal America. Of this number, four species belonging to as many genera have been recognized in the larval state. Another unidentified species, feeding on pecan, is added in this paper. Dyar (1898) described the larvae of *Megaxyela major* and *Xyela minor* and gave a definition of the family based on characters found in these species. He pointed out that they are most nearly related to the Pamphiliidae. The larvae of *Odontophyes aviingrata* were described by the same author (1899). Konow (1901) overlooked Dyar's 1898 paper and gave in his analytical table for the larvae *Odontophyes aviingrata* as the sole representative of the subfamily Xyelini. That Konow was unfamiliar with any xyelid larvae may be reasonably assumed from the fact that he classified them with those larvae which had no larvapods and that he placed a question mark before the analytical item "ohne Afterborsten." The larvae of *Pleuroneura*, *Paraxyela* and *Protoxyela* are unknown. The described larvae feed on the foliage of hickory, butternut, pecan, elm, and the staminate flowers of pine.

The most important materials that I had in the study of this family were received from Professor R. W. Harned, of the Mississippi Agricultural College, but, altogether, the material at hand is so limited that it does



not permit a characterization of the genera. The following key will serve to separate the species:

- 1(8) Larvapods present on all abdominal segments, those on the first and ninth segment sometimes rudimentary; thoracic legs normal in form; body tuberculate, tubercles setiferous, concolorous with the head; head creamy or brownish or blackish; abdominal segments typically with four annulets, first annulet smooth, non-tuberculate, crescentic, and confined to the dorsal aspect, three following annulets convex, with transverse row of setiferous tubercles; not on staminate flowers of conifers. . . . . 2.
- 2(7) Head dark-colored, brownish or blackish; tenth abdominal tergum always and prothoracic and ninth abdominal terga usually with dark-colored patches; tenth tergum brownish or blackish; subanal lobe with a pair of wart-like brown tubercles which bear blackish brown setae on the dorsal and lateral aspects, less densely on the ventral aspect; dorsal tubercles arranged typically as follows: the second and third annulets with four to five, the fourth annulet with two or three; the subspiracular and surpedal lobes, each with a tubercle; the dorsal tubercles of the second annulet with one to three setae. . . . . 3.
- 3(6) Tubercles of typical abdominal segment arranged as follows: second and third annulets with four tubercles above the spiracular line, each tubercle bearing one seta, the fourth annulet with two tubercles, one on the spiracular line with two setae, the other, dorsad of the line, with one seta; on hickory and pecan. . . . . 4.
- 4(5) Prothoracic tergum with a large dark brown, median patch whose lateral margins converge toward the cephalic margin, which is one-half as long as the caudal margin; the ninth abdominal tergum with a large dark brownish patch on each side of the meson, the patches converging toward the caudal margin so that the caudal halves are nearly confluent on the meson with a pair of brownish tubercles between the cephalic halves; tenth abdominal tergum almost completely dark brown in color; the first annulet of typical segment with the dorsal pair of tubercles quadrate, one-half as long as the annulet; abdomen with a brownish, cloudy, longitudinal dorso-lateral line involving the dorsal pair of tubercles and extending usually from the second abdominal segment to the seventh; on hickory and pecan; Y-226, G. . . . .  
*Megaxyela major* Cresson.
- 5(4) Prothoracic tergum without a large dark brownish median patch, but with a pair of small blackish patches distinctly separated on the meson of the first and second annulets, the cephalic pair larger, triangular, and their apices directed laterad, the caudal pair subquadrate, further apart than the cephalic pair; the ninth abdominal tergum without a pair of large dark brownish patches but with two pairs of small blackish patches, distinctly separated on the meson, the cephalic pair smaller and slightly further apart than the caudal pair; tenth tergum blackish, with its cephalic constricted portion pale or creamy; first annulet of typical abdominal segment with the dorsal pair of tubercles subcircular, one-third as long as the annulet; abdomen without a brownish, cloudy longitudinal dorso-mesal lines; on pecan; Y-227. . . . .  
*Megaxyela* sp. 1.
- 6(3) Tubercles of a typical abdominal segment arranged as follows: second and third annulets with four to five tubercles above the spiracular line, each tubercle bearing two setae; the fourth annulet with three tubercles, one on the spiracular line and the other two dorsad of it, each tubercle with two setae; on hickory and butternut; Y-228. . . . . *Odontophyes aviingrata* Dyar.
- 7(2) Head light in color, creamy white or pale brown; the prothoracic and the ninth and tenth abdominal terga without dark-colored patches; tenth tergum light brown; subanal lobe with a pair of wart-like creamy tubercles which bear long light brown



- setae, uniformly distributed on all aspects; tubercles arranged as follows: the second and third annulets with four tubercles dorsad of the spiracular line, the second tubercle dorsad of the ventral one sometimes rudimentary and often represented by a single tiny seta, the fourth annulet with two tubercles, one on the spiracular line and the other dorsad of it, the sublateral area divided into three lobes and each with one tubercle; the dorsal pair of tubercles of the first annulet with four to five setae; on *Ulmus*; *G.*..... *Macroxyela ferruginea* Say.
- 8(1) Larvapods very small; thoracic legs rudimentary; body not tuberculate; head creamy white; abdominal segments typically with three annulets; on staminate flowers of pine (Dyar in 1898 described no larvapods)..... *Xyela minor* Dyar.

#### FAMILY BLASTICOTOMIDAE

The Blasticotomidae contains a single genus and species, *Blasticotoma filiceti* Klug, which is confined to central and eastern Europe. It is an archaic type. The systematic position of this unique species has been considered differently by practically every writer who has studied it. MacGillivray (1906) has shown, however, that it is in certain of its characters closely allied to the Xyelidae and Pamphiliidae, while in others it approximates the Tenthredinidae, and that, it is intermediate in position between these two groups.

Because of its taxonomic position, it is highly desirable to know the characters of the larvae of this species, but unfortunately the literature is void of information in regard to the immature stages, and this interesting quest must await future discoveries.

#### FAMILY TENTHREDINIDAE

Larvae (Figs. 7-25) very small to very large, length 10-40 mm.; caterpillar-like, leaf-feeders, leaf-miners, or fruit-borers; body cylindrical, thorax usually largest in diameter, body tapering caudad, sometimes flattened on the ventral aspect, leaf-miners depressed; greenish or variously colored with or without distinct markings; smooth, glabrous, setiferous, tuberculate, or spinous; segmentation usually and annulation sometimes distinct; third abdominal segment with 6, 7, 5, 4, 3, or 2 annulets, mentioned in the order of frequency; some of annulets usually setiferous and often with glandulae; thoracic legs always present, usually well developed, typically with five segments, sometimes with three, four, or six segments, but always with distinct tarsal claws; legs rarely rudimentary, fleshy, indistinctly segmented, and without tarsal claws; larvapods present usually on abdominal segments 2-7 and 10 or 2-8 and 10, occasionally the seventh and tenth pairs wanting, rarely with all larvapods obsolete; head typically semiglobose, setiferous, with or without distinct markings or uniformly brownish, blackish, or greenish; antennae always present, never with more than five segments; ocellaræ always present, one on each side;

maxillary and labial palpi typically with four and three segments respectively, never obsolete, number of segments rarely reduced; clypeus usually with two or three setae on each side; mandibles usually with one to four setae; tenth abdominal tergum without suranal process and sometimes with caudal protuberances; subanal appendages never present; epicranial suture and vertical furrows usually present; metaspiracles functionless, obsolete, or very much smaller than abdominal spiracles; various glands sometimes present.

The family Tenthredinidae according to MacGillivray contains twenty-four subfamilies of which five are not represented in the Nearctic fauna. The subfamilies found in the United States and Canada are as follows: Diprioninae, Emphytinae, Selandriinae, Dolerinae, Phyllotominae, Lycaotinae, Tenthredininae, Cimbicinae, Hoplocampinae, Dineurinae, Monocteninae, Cladiinae, Nematinae, Blennocampinae, Fenusinae, Scolioneurinae, Hylotominae, Schizocerinae, and Acordulecerinae. Of these, Lycaotinae and Dineurinae have not been available for study.

#### SUBFAMILIES OF TENTHREDINIDAE

- |        |   |                           |
|--------|---|---------------------------|
| 1(42)  | Thoracic legs normal in form, five-segmented; if modified, tarsal claws always present; larvapods usually well developed.....   | 2.                        |
| 2(23)  | Larvapods present on abdominal segments 2-8 and 10; antennae elongate, conical, usually with five segments.....   | 3.                        |
| 3(20)  | Thoracic legs with five segments, normal in form.....   | 4.                        |
| 4(11)  | Third abdominal segment with six annulets on dorsum.....  | 5.                        |
| 5(10)  | Antennae conical, with five segments.....   | 6.                        |
| 6(9)   | Labrum bilaterally symmetrical; legs with tibia shorter than femur, tarsal claws short, strongly curved.....  | 7.                        |
| 7(8)   | Body rather slender, tapering caudad, without small distinct tubercles; tenth abdominal tergum without small tubercles; head never shiny, jet-black, body never yellowish white.....                  | EMPHYTINAE (in part).     |
| 8(7)   | Body rather robust, uniform in diameter thruout, with small distinct tubercles; tenth abdominal tergum with several small protuberances, if without, head shiny, jet-black, body yellowish white..... | BLENNOCAMPINAE (in part). |
| 9(6)   | Labrum not bilaterally symmetrical, but distinctly asymmetrical; legs with tibia longer than femur, tarsal claws slender, only slightly curved.....   | DOLERINAE.                |
| 10(5)  | Antennae not conical, with three segments, the third segment erect and peg-like.....  | DIPRIONINAE.              |
| 11(4)  | Third abdominal segment with more or less than six annulets on dorsum.....  | 12.                       |
| 12(19) | Third abdominal segment with seven annulets on dorsum; body without conspicuous branched spines or tubercles.....   | 13.                       |
| 13(18) | Antennae conical, with five segments; labrum without secondary longitudinal sutures.....  | 14.                       |
| 14(15) | Larvapods setiferous; clypeus with three setae on each side; mandible with two setae; labrum without a median longitudinal depression.....  | SELANDRIINAE (in part).   |
|        |   | EMPHYTINAE (in part).     |
| 15(14) | Larvapods glabrous; clypeus with two setae on each side; mandible with 1-4 setae; labrum with or without a median longitudinal depression.....  | 16.                       |

- 16(17) Legs with tibia minute, distinctly shorter and smaller than femur; maxillae with stipes without cephalo-ventral triangular projection; mandibles with two setae; labrum without a median longitudinal depression.....17.  
SELANDRIINAE (in part).
- 17(16) Legs with tibia large, usually subequal to or longer than femur; maxillae with stipes with cephalo-ventral triangular projection; mandibles with 1, 2, or 3-4 setae; labrum with or without a median longitudinal depression.....TENTHREDININAE.
- 18(13) Antennae not conical, with one segment; labrum with secondary longitudinal sutures; small but distinct crescentic glandubae dorsad of spiracles. CIMBICINAE.
- 19(12) Third abdominal segment with five, rarely three or four, annulets on dorsum; body with conspicuous branched spines or tubercles. BLENNOCAMPINAE (in part).
- 20(3) Thoracic legs with four segments, modified.....21.
- 21(22) Tenth urotergum and prothoracic and mesothoracic tergites with conspicuous fleshy pointed protuberances; body not tadpole-like.....EMPHYTINAE (in part).
- 22(21) Tenth urotergum and prothoracic and mesothoracic tergites without conspicuous fleshy pointed protuberances; body often distinctly tadpole-like.  
PHYLLOTOMINAE (in part).
- 23(2) Larvapods on abdominal segments 2-7 and 10, rarely on segments 2-7 or 2-6 and 10.....24.
- 24(39) Thoracic legs with five segments, normal in form; larvapods on segments 2-7 and either with or without anal larvapods.....25.
- 25(36) Larvapods present on the ultimate segment, either normal and separated or fused on the meson, forming a single prominence.....26.
- 26(35) Anal larvapods normal and separated.....27.
- 27(28) Antennae with five segments; third abdominal segment with six annulets; tenth abdominal tergum with several caudal protuberances. HOPLOCAMPINAE (in part).
- 28(27) Antennae with four, rarely three, segments; third abdominal segment usually with less than six annulets; tenth abdominal tergum with or without caudal protuberances.....29.
- 29(32) Abdominal segments 1-7 on ventro-meson with an eversible gland; body often with numerous conspicuous setae, setae arising from distinct tubercles; antennae with four segments.....30.
- 30(31) Body with numerous conspicuous multisetiferous tubercles, each tubercle bearing several long setae, some of which are distinctly longer than others; third abdominal segment with four annulets, annulet 1 with a transverse row of setae, annulets 2 and 3 with a transverse row of setiferous tubercles; tenth abdominal tergum never with caudal protuberances altho with numerous long setae; setae barbed. CLADIINAE.
- 31(30) Body without numerous conspicuous multisetiferous tubercles, if tubercles present, they do not bear several long setae some of which are distinctly longer than others; third abdominal segment with varying number of annulets; tenth abdominal tergum sometimes with caudal protuberances; setae not barbed.....NEMATINAE.
- 32(29) Abdominal segments 1-7 on ventro-meson without an eversible gland; body never conspicuously setiferous; antennae with three or four segments; third abdominal segment with three or five annulets.....33.
- 33(34) Antennae with four segments; third abdominal segment with five annulets; abdominal segments 2-4 and 8 or 2-5 and 8 without a postsubspiracular sucker-like protuberance.....HOPLOCAMPINAE (in part).
- 34(33) Antennae with one segment; third abdominal segment with three annulets; abdominal segments 2-4 and 8 or 2-5 and 8 each with a postsubspiracular sucker-like protuberance.....ACORDULECERINAE.



- 35(26) Anal larvapods united on the meson forming a single protuberance; antennae with one segment; third abdominal segment with two annulets; prothorax often with dorsal and ventral shields; vertical furrows wanting; head and body depressed, glabrous. .... SCOLIONEURINAE.
- 36(25) Larvapods wanting on ultimate segment; vertical furrows wanting. .... 37.
- 37(38) Antennae with three segments; third abdominal segment with four annulets, annulets 2 and 3 setiferous; tenth abdominal tergum with a caudo-mesal protuberance; body not depressed. .... HOPLOCAMPINAE (in part).
- 38(37) Antennae with 1-2 segments; third abdominal segment with two annulets, annulets glabrous; tenth abdominal tergum without a caudo-mesal protuberance; body depressed. .... FENUSINAE.
- 39(24) Thoracic legs with 3-4 or 6 segments; larvapods on abdominal segments 2-7 and 10 or 2-6 and 10, very small. .... 40.
- 40(41) Mesothoracic and metathoracic legs with six segments; prothoracic legs with six segments; larvapods on abdominal segments 2-7 and 10 and occasionally with a rudimentary eighth pair, or 2-6 and 10; body dilated laterad, sublateral lobe produced and conspicuous, often with numerous setiferous tubercles. HYLOTOMINAE.
- 41(40) Mesothoracic and metathoracic legs with three segments; prothoracic legs with four segments; larvapods on abdominal segments 2-7 and 10 with an occasional rudimentary eighth pair; body not dilated laterad, sublateral lobe not produced and conspicuous; body never with numerous setiferous tubercles but with minute protuberances. .... SCHIZOCERINAE.
- 42(1) Thoracic legs not normal in form, but fleshy, indistinctly four-segmented, tarsal claws wanting; larvapods vestigial on abdominal segments 2-8 and 10, ultimate pair united on the meson, forming a single protuberance. ....  
PHYLOTOMINAE (in part).

#### SUBFAMILY DIPRIONINAE

Larvae (Fig. 7) moderately large, length 18-25 mm.; body cylindrical, somewhat robust, tapering gradually caudad; segmentation and annulation distinct; third abdominal segment with six annulets, annulets 1, 2, and 4 or 2 and 4 with setae and glandubae; larvapods on abdominal segments 2-8 and 10, close together on the meson; thoracic legs normal, well developed, with five segments; prothoracic legs distinctly smaller than other legs; color of body usually yellowish or greenish, with grayish, or brownish stripes or rows of black spots; antennae with three segments, segments 1 and 2 minute, flat, irregular, incomplete, segment 3 erect, peg-like, strongly chitinized; head and legs usually with spinous, stiff setae; glandubae prominent and numerous; ventral glands wanting; spiracles not winged; cuticle microscopically spinulate; larvae feed on conifers.

The subfamily Diprioninae is represented in North America by three genera, *Diprion*, *Neodiprion*, and *Monoctenus*. The Nearctic species formerly placed in the genus *Diprion* (*Lophyrus*) are placed by Rohwer (1918a) in *Neodiprion*. *Diprion simile* Hartig of Europe has recently become established in the United States. With the exception of MacGillivray, systematists agree in associating the genus *Monoctenus* with *Diprion* and its allies.



The three genera studied can be separated as follows:

- 1(2) Body large, stout, longer than 24 mm.; markings mottled with dark brown and yellowish irregular spots, without brownish stripes or black spots; setae on head small, slender, those on genae similar to other setae, not spinous; head blackish.  
*Diprion* Schrank.
- 2(1) Body smaller, slender, usually shorter than 24 mm.; markings not mottled, but with brownish longitudinal stripes or rows of black spots. .... 3.
- 3(4) Third abdominal segment with annulets 1, 2 and 4 with setae and glandubae; setae on head stiff, long, spinous, those on genae often very large and spinous. ....  
*Neodiprion* Rohwer.
- 4(3) Third abdominal segment with annulets 2 and 4 with setae and glandubae; setae on head microscopic, and very few in number. .... *Monoctenus* Dahlbom.

#### NEODIPRION ROHWER

Larvae rather large; length about 19–24 mm.; body slender, with longitudinal brownish stripes or rows of black spots along subdorsal, supra-spiracular, and sometimes subspiracular lines; head round in contour, cephalic and caudal margins parallel in profile; front flattened, subpentagonal, as high as wide; ocularia large; antennaria subequal in diameter to ocularia, their own diameter apart; labrum semicircular, with small crescentic median emargination; mandibles sharply dentate, the dextral with four dentes and the sinistral with five; maxillary palpi large, four-segmented, segments 1-3 ring-like, successively diminishing in diameter, segment 4 suddenly and distinctly smaller than the preceding segment, conical, bluntly pointed; galea chitinized, digit-like, smaller than palpi; lacinia thick, lobate, bearing a minute triangular blade-like seta on ventro-mesal angle, a stiff seta on dorso-mesal angle, and a row of three to five minute setae on the oblique cephalo-mesal margin; labial palpi normal, segment 2 usually longest, segment 3 conical, suddenly and distinctly smaller than preceding segment; totaglossa with dorso-cephalic depression on the meson and with several minute sensory pits; parapharynx distinct, linguiform, constricted dorsad of the middle by a pair of chitinized pieces; thoracic legs well developed, normal in form, usually blackish, segments strongly chitinized, coxae largest, trochanter ring-like, chitinized on the caudal two-thirds, with a whorl of setae, distad of setae membranous, femur smaller than trochanter in diameter, entirely chitinized, wider than long on dorsal aspect, increasing in diameter distad, tibia subequal in length to femur but smaller in diameter, tarsal claws small, basal portion of claw undeveloped, all segments of leg membranous on the ventral aspect, prothoracic legs one-half the size of metalegs, mesolegs slightly smaller than the latter; third abdominal segment with annulation formula, 2, 1, (3, 5, 6), 5; spiracle on annulet 2, annulets 1, 2 and 4 with a transverse row of slender, cylindro-conical glandubae, annulet 2 with a few microscopic setae; substigmatal and surpedal lobes large, with several glandubae

and a few setae; larvapods well developed, distal surface incurved mesad, rather dilated, not pointed, distance between the pair at the base less than the length of larvapod, venter with four annulets; tenth abdominal tergum gradually convex, with glandubae; anal setae numerous, small; spiracles elongate and oblong.

#### SPECIES OF NEODIPRION

- 1(10) Head black, light grayish or brownish, never uniformly reddish brown or orange; body longitudinally striped or spotted. ....2.
- 2(3) Body with four longitudinal rows of black spots along subdorsal and supraspiracular lines; tenth abdominal tergum with cephalic two-thirds entirely black; spots on each side of dorso-meson elongate, wider at cephalic end; spots on supraspiracular line large, subquadrate; spots on prothorax obsolete; body yellowish white; length, 22 mm.; on *Pinus*; Y-221, G-573, C-1, I-4101. .... *abbottii* Leach.
- 3(2) Body without four longitudinal rows of black spots along the subdorsal and supraspiracular lines, but with longitudinal colored bands along each side of the dorso-meson; latus with longitudinal row of independent segmentally arranged blackish or brownish spots or with continuous brownish bands. ....4.
- 4(5) Body with a row of brownish spots along supraspiracular lines, spots segmentally arranged, one on each segment, often those on middle segments obsolete, sometimes all spots obsolete; tenth abdominal tergum with a pair of large blackish or brownish spots which are all sometimes contiguous on meson; subdorsal bands narrower than the distance between them; larvapods marked faintly along pedal line when supraspiracular spots are distinct; head black; length, 23 mm.; G-1686-2, -5. *Neodiprion* sp. 1.
- 5(4) Body with broad longitudinal bands along supraspiracular lines, instead of rows of segmentarily arranged spots. ....6.
- 6(7) Subspiracular lines with broad brownish bands; head black; pedal lines also marked brown; tenth abdominal tergum faintly marked; subdorsal bands much wider than the distance between them; these bands much lighter in color than those on latus; body dull greenish; length, 21 mm.; on spruce; G-791. .... *abietis* Harris.
- 7(6) Subspiracular lines without brownish bands; head light brown, brown, or pale creamy yellow; subdorsal bands very narrow or very wide; pedal lines with or without bands. ....8.
- 8(9) Pedal lines with distinct brownish bands; tenth abdominal tergum unmarked except along caudal margin; subdorsal bands very much wider than the distance between them, lighter in color; head blackish or brownish with brown marks on vertex and front or pale brown; length, 19 mm.; G-156. .... *Neodiprion*, sp. 2.
- 9(8) Pedal lines without distinct brownish bands; tenth abdominal tergum marked, entirely concolorous with head; subdorsal bands very narrow, usually narrower than the distance between them; head light brown or pale creamy white with vertex shaded grayish; length, 19 mm.; G-1686-3, -6, -7. .... *Neodiprion* sp. 3.
- 10(1) Head reddish brown or orange; body spotted; subdorsal and supraspiracular lines with black spots. ....11.
- 11(12) Subspiracular and pedal lines with black spots; spots on subdorsal lines tapering caudad, partly broken between annulets; spots along supraspiracular lines large, subquadrate; spots on subspiracular lines smaller, sometimes very small but never obsolete; spots on pedal lines very small, sometimes obsolete; tenth abdominal tergum with a pair of large black spots which sometimes fuse on the meson; length, 25-28 mm.; G-1554, -1686-8, -593, C-cue-315, C-Young-37. .... *lecontei* Fitch.

- 12(11) Subspiracular and pedal lines without black spots; spots on subdorsal lines small, often not distinctly tapering caudad; tenth abdominal tergum with a pair of large black spots; length, 20 mm.; G-133.....*Neodiprion*, sp. 4.

### MONOCTENUS DAHLBOM

Larvae rather small; length about 15 mm.; body slender, dorsum with diffuse brownish shade or with longitudinal stripes; third abdominal segment with annulets 2 and 4 with setae and glandubae; head as in *Neodiprion* except that setae are minute and sparse; clypeus and labrum with two setae on each side; labrum with small crescentic median emargination; maxillary palpi large, rather slender, segments 1-3 ring-like, subequal in length but successively smaller in diameter; galeae and laciniae as in *Neodiprion*; labial palpi rather slender, its segments subequal in length; mandible with one mandibular seta; antennae with segment 1 complete, very narrow, oval, segment 2 flat, incomplete, irregular, segment 3 peg-like, erect; glandubae conical, distinct; setae microscopic; sublateral lobes not well developed; annulation typically (1, 2), (3, 4, 5, 6), anal setae numerous, short, and minute; telson with glandubae obsolete.

MacGillivray established in 1906 the subfamily Monocteninae for the genus *Monoctenus* associating it with the Cladiinae and Nematinae, thus deviating from the universal practice of regarding the genus *Monoctenus* as a member of the subfamily Diprioninae or its equivalent. On the basis of the venation, MacGillivray's contention is quite justifiable, and it is most interesting to know what larval characters would indicate in regard to the relationship between *Monoctenus* and *Diprion* and its allies. Marlatt (1887) published notes on the immature stages of *Monoctenus unicolor* but his descriptions do not touch the detailed anatomy necessary for the definition of the genus. Recently, however, I was fortunate enough, thru the courtesy of Mr. Rohwer, to examine a specimen belonging to the United States National Museum which Rohwer considered to belong to a new species of *Monoctenus*. A careful study of this larva convinced me that [so far as this species is concerned] there are no essential differences between the larvae of *Monoctenus* and those of the typical Diprioninae to justify the creation of a new subfamily. For this reason I have followed the universal practice and decided to treat *Monoctenus* as a member of the Diprioninae.

*Monoctenus* n. sp. Rohwer.—Length, 14 mm., head-width 1.5 mm.; head brownish; body on dorsum dorsad of spiracular lines, segments of legs, episternum and epimeron, deep brown; glandubae elongate, conical, minute, brownish at tip; on cedar.

A specimen bearing the label "5419 Sawfly on cedar, Cadek, Mo., June 10, 1892."



## DIPRION SCHRANK

As far as known, only one species is represented in North American fauna. An examination of *D. simile* shows that this genus is not very different from the other genera of Diprioninae but may be separated from them by the characters of the setae and coloration of the head, and certain minor points. It is not possible to characterize the genus with the material at hand.

*Diprion simile* Hartig.—Body robust, length, 25 mm.; latus with a series of yellowish or whitish spots on a uniformly grayish brown background, dorso-meson with a narrow yellowish stripe bordered on each side by an equally narrow grayish brown band; dorso-lateral lines broadly yellowish, interrupted at each annulet by fine transverse lines; supraspiracular lines with three yellow spots, size of spots increasing caudad; dorsad of these, three smaller spots with the middle one largest and subequal to cephalic spot of supraspiracular lines; three spots on subspiracular lines, the middle one being the largest; pedal lines with a large spot on each segment; larvaped with a brownish spot; tenth abdominal tergum and sternum marked with grayish; the tergum with a deep constriction dorsad of suranal lobe; head setae small, slender, hair-like, never spinous or stiff; setae on genae similar to those on front, never stiff and spinous; legs with femur sometimes longer than wide on the dorsal aspect; head black; body yellowish gray, mottled; G.

## SUBFAMILY EMPHYTINAE

Larvae (Fig. 8) small to moderately large, usually greenish, sometimes striped; body cylindrical, slender, tapering caudad; segmentation distinct, annulation fine, indistinct; third abdominal segment usually with six, rarely seven, annulets, annulets 2 and 4 or 1, 3, 5 and rarely 1, 3, and 6 setiferous; head greenish or brownish; sometimes with spots on vertex and front; labrum with or without a mesal longitudinal depression, with 4-5 labral setae on each side of the meson; clypeus with 2 or 3 setae on each side; mandibles with one seta rarely with two; larvaped on abdominal segments 2-8 and 10, well developed, usually glabrous, rarely setiferous; ventral glands wanting; glandubae small, conical, on annulets 1 and 3 or rarely on 2 and 4; tenth abdominal tergum usually setiferous but without paired caudal protuberances, rarely with conspicuous spines on the caudal margin, if spines present, then prothorax and mesothorax on dorsum with two and one protuberances respectively; antennae elongate-conical, with five segments, segments ring-like; thoracic legs usually normal in structure, with femur subequal in length to or slightly longer than tibia, tibia well developed and normal, femur with its disto-ventral angle produced; legs, when modified, short, stout, and trochanter obsolete; mouth-parts normal in form, spiracles not winged; larvae leaf-feeders.



The Emphytinae is a large subfamily embracing a number of genera and numerous species. MacGillivray considers this the second subfamily of his generalized Tenthredinidae and places it between the Diprioninae and Selandriinae. The larvae of this subfamily are found readily and in general appearance and habitus resemble very closely the larvae of the Selandriinae and Tenthredininae, but they can be separated by the number of annulets, which in this subfamily, with the exception of *Hemitaxonus* and *Epitaxonus*, is six, while in the other two subfamilies it is seven. The two genera mentioned are characterized by the presence of seven annulets on the typical abdominal segment and also by the setiferous larvopods, thus resembling in these two particulars the larvae of the Selandriinae. It is of interest to note that Rohwer would associate *Hemitaxonus* with such genera as *Selandria*, *Eriocampoides*, etc., in the tribe Selandriini of his subfamily Selandriinae. Middleton (1915) has published a definition of the genus *Dimorphopteryx* together with a key for the separation of three species.

The writer has collected a large number of larvae belonging to this subfamily, but on account of the difficulty of breeding adults many species remain unidentified. In the preparation of the synoptic key to the genera and in discussions following, only bred or otherwise identified species have been considered, the consequence being that future study may require much modification in our conception of the various genera dealt with.

#### GENERA OF EMPHYTINAE

- |       |   |                                 |
|-------|---|---------------------------------|
| 1(4)  | Third abdominal segment with 7 annulets; larvopods setiferous. . . . .  | 2.                              |
| 2(3)  | Larvopods with 5-3-1 setae on cephalic, lateral, and caudal aspects respectively; thoracic legs with femur longer than or subequal to tibia; labial palpi with segment 2 longer than segment 1; maxillary palpi with segments subequal in length. . . . . |                                 |
|       |   | <i>Hemitaxonus</i> Ashmead.     |
| 3(2)  | Larvopods with 8-5-1 setae on cephalic, lateral, and caudal aspects respectively; thoracic legs with femur shorter than tibia; labial palpi with segments subequal to each other in length; maxillary palpi with segment 2 longer than segment 1. . . . . |                                 |
|       |   | <i>Epitaxonus</i> MacGillivray. |
| 4(1)  | Third abdominal segment with 6 annulets; larvopods glabrous. . . . .  | 5.                              |
| 5(26) | Tenth abdominal tergum and prothoracic and mesothoracic tergites without conspicuous fleshy pointed protuberances; thoracic legs normal in form, with trochanters distinct. . . . .   | 6.                              |
| 6(9)  | Annulets 1, 2, and 4 setiferous. . . . .  | 7.                              |
| 7(8)  | Antennae with segment 5 longest; legs with femur longer than tibia; head usually without markings; labial palpi, if segments not subequal, segment 2 longer than segment 1. . . . .   | <i>Empria</i> Lepeletier.       |
| 8(7)  | Antennae with segment 1 longest; legs with femur subequal to tibia; head usually with markings; labial palpi, if segments not subequal, segment 2 shorter than segment 1. . . . .   | <i>Parataxonus</i> MacGillivray |
| 9(6)  | Annulets 2 and 4 setiferous. . . . .  | 10.                             |

- 10(11) Clypeus with three setae on each side of meson; mandibles with two setae; maxillae with palpi produced dorsad as a triangular lobe; labrum with a deep median emargination with a row of secondary setae caudad of the emargination. . . . .  
*Eriocampa* Hartig.
- 11(10) Clypeus with two setae on each side of meson; mandibles with one seta; maxillae with palpi not produced dorsad as a triangular lobe; labrum without a deep median emargination. . . . . 12.
- 12(13) Thoracic legs with trochanter longer than tibia. . . . . *Strongylogastroidea* Ashmead.
- 13(12) Thoracic legs with trochanter distinctly shorter than tibia. . . . . 14.
- 14(15) Body spotted or transversely striped; head dorsad of ocellaræ entirely blackish or brownish; very large and robust larvae. . . . . *Macremphytus* MacGillivray.
- 15(14) Body never spotted or transversely striped; head dorsad of ocellaræ not entirely blackish or brownish; smaller larvae. . . . . 16.
- 16(17) Labial palpi with segment 1 longer than segment 2; legs with femur always longer than tibia; tibia usually twice as long as trochanter; body rather robust; head not marked distinctly with brown; annulet 4 longest on third abdominal segment. . . . .  
*Monostegia* Costa.
- 17(16) Labial palpi with segment 1 shorter than segment 2; legs with femur not always longer than tibia; tibia always more than twice as long as trochanter; body rather slender; annulet 4 not longest on third abdominal segment. . . . . 18.
- 18(19) Head entirely pale, no markings; legs with femur longer than tibia; body on dorsum not shaded darker than the venter; tenth abdominal tergum not marked. . . . .  
*Monosoma* MacGillivray.
- 19(18) Head not entirely pale, usually with brown spots or markings; legs with femur not always longer than tibia, often subequal; body on dorsum sometimes shaded darker than the venter; tenth abdominal tergum often marked. . . . . 20.
- 20(21) Legs with femur always longer than tibia; tenth abdominal tergum usually marked; body on dorsum usually shaded darker than the venter. . . . . *Emphytus* Klug.
- 21(20) Legs with femur subequal to or shorter than tibia; tenth abdominal tergum usually unmarked; body on dorsum not usually shaded darker than the venter. . . . . 22.
- 22(23) Tenth abdominal tergum marked with a spot; body on dorsum shaded darker than the venter; labial palpi with segment 2 longer than segment 1. . . . .  
*Unitaxonus* MacGillivray.
- 23(22) Tenth abdominal tergum unmarked; body on dorsum not shaded darker than the venter; labial palpi with segment 2 subequal to or shorter than segment 1. . . . . 24.
- 24(25) Labrum with a distinct median depression. . . . . *Taxonus* Hartig.
- 25(24) Labrum without a distinct median depression. . . . . *Phrontosoma* MacGillivray.
- 26(5) Tenth abdominal tergum and prothoracic and mesothoracic tergites with conspicuous fleshy pointed protuberances; thoracic legs not normal in form, with trochanters obsolete. . . . . *Dimorphopteryx* Ashmead.

## SUBFAMILY SELANDRIINAE

Larvae (Fig. 9) small to fairly large, length 18-26 mm.; body cylindrical and gradually tapering caudad; segmentation and annulation distinct and fine; larvapods on abdominal segments 2-8 and 10; third abdominal segment with seven annulets, annulets 1, 3, and 5 setiferous, annulets 3 and 5 with glandubae; thoracic legs normal in form except tibia sometimes very minute; body uniformly greenish, without colored markings; head with or without brownish spots; antennae with five segments, long, conical;

mouth-parts normal in form, well developed, palpi large; mandibles with two setae; clypeus with three, sometimes four, setae on each side, rarely with two; stipes of maxillae with triangular cephalo-ventral projection; glandubae minute, stalked; spiracles not distinctly winged; larvapods setiferous, with about ten setae, rarely glabrous.

The Selandriinae includes a limited number of genera. On the basis of the venation this subfamily is placed next to the Emphytinae where practically all systematists have placed it. Rohwer's conception of this subfamily is somewhat different from that of MacGillivray and therefore he differs from the latter in the disposition of some of the genera. For example, Hemitaxonus is assigned to the tribe Selandriini while MacGillivray placed it, together with Epitaxonus, in the Emphytinae. It may be said that the larvae of these two genera are very closely related to the Selandriinae and differ from all other Emphytinae in the typical number of annulets.

GENERA OF SELANDRIINAE

- 1(4) Thoracic legs with tibia normal in form, never greatly reduced, usually subequal in length to femur; larvapods setiferous; clypeus with three or four setae on each side.....2.
- 2(3) Tenth abdominal tergum with brown spots; larvapods usually with ten or more setae; clypeus usually with three and often four setae on each side; labium deep brown, with four to six setae on each side; glandubae slightly longer than one-half the length of adjacent setae; spiracles not winged; larger larvae; length more than 24 mm.....*Thrinax* Konow.
- 3(2) Tenth abdominal tergum not marked with brown spots; larvapods usually with less than ten setae; clypeus with three, rarely with four, setae on each side; labium pale brown or whitish with three to six setae; glandubae usually subequal in length to adjacent setae; spiracles faintly winged; smaller larvae; length less than 24 mm.  
*Strongylogaster* Dahlbom.
- 4(1) Thoracic legs with tibia reduced, very much smaller than femur; larvapods glabrous; clypeus with two setae on each side.....*Selandria* Leach.

THRINAX KONOW

Larvae comparatively large, long, length more than 24 mm.; body slender, finely annulate, uniformly greenish; head and tenth abdominal tergum with brown markings; thoracic legs normal, tibia and femur cylindrical, tapering caudad, subequal in length; larvapods with about ten setae, distributed as follows: 4-5 on cephalic and lateral aspects and one on caudal; clypeus usually with three and often with four setae on each side; labrum with four to six setae on each side, deep brown, without median longitudinal depression; glandubae small, very short, slightly longer than one-half the length of adjacent setae; spiracles not winged; maxillary palpi with segments 2 and 4 subequal in length; labial palpi with segment 4 longer than segment 3; ninth abdominal tergum with six annulets, annulets 1, 3, and 5 setiferous, annulet 6 a little shorter than the second.



## SPECIES OF THRINAX

Head pale brown with vertex marked with brown on dorsum and caudad of ocellaræ, front with a round brown spot contiguous to ventral apex of the dorsal marking on the vertex, frontal spot not reaching the fronto-clypeal suture; antennæ, mouth-parts, femur, tibia, and tarsal claw deep brown; tenth abdominal tergum with a pair of small brown spots; annulation formula, 1, (5, 4, 3), 2, (6, 7); antennæ, 5, 4, 3, 2, 1; labial palpi with distal two segments subequal; legs with trochanter, femur, and tibia with lengths to each other as 12, 15, and 16 respectively; tarsal claws with the proximal portion shorter than the distal narrow curved portion; length 26 mm.; width of head 2 mm.; on fern; M-18.....*impressatus* Provancher.

Head pale brown with vertex marked with brown on dorsum and caudad of ocellaræ, front with a subquadrate spot contiguous to the ventral apex of dorsal marking of the vertex, frontal spot reaching the fronto-clypeal suture; antennæ, labrum, mouth-parts, femur, tibia, and tarsal claw deep brown; tenth abdominal tergum with a pair of large brown spots; annulation, 1(5, 4, 3, 1), (6, 7); antennæ, 5, 4, 1, 3, 2; labial palpi with distal segment longer than the preceding; legs with trochanter, femur, and tibia with lengths to each other as 12, 15 and 16 respectively; tarsal claws with the proximal portion as long as the distal curved portion; length 25 mm.; width of head, 2 mm.; on fern; Y-20-3-1, -20-1.....*pulatus* MacGillivray.

## STRONGYLOGASTER DAHLBOM

Larvæ small comparatively speaking, length less than 24 mm.; body slender, finely annulate, uniformly green; head pale or light brown or sometimes with a few spots; tenth abdominal tergum never distinctly marked; larvæpods usually with less than ten setæ; thoracic legs normal in form, femur and tibia subequal to each other or one longer than the other; labrum pale brown or whitish, with three to six setæ on each side; glandulæ usually subequal in length to adjacent setæ; spiracles often faintly winged.

## SPECIES OF STRONGYLOGASTER

- 1(2) Head with blackish brown markings, vertex with a pair of diverging spots over the vertical furrows directed toward ocellaræ and a spot caudad of each ocellaræ; vertical markings sometimes faint, sometimes very distinct and large, merging into a continuous vertical marking; front never with spot; antennæ, labrum, and mouth-parts light brown; tenth abdominal tergum usually without markings, rarely with a pair of faint spots; annulation, 1, 4, (2, 3, 5), (6, 7); antennæ, 1, 5, (2, 3, 4); maxillary palpi, 2, (1, 4), 3; labial palpi with two distal segments equal in length to each other, shorter than distal segment of maxillary palpi; labrum with three or four setæ on each side; mandible with two, rarely three, setæ; legs with trochanter, femur, and tibia with lengths to each other as 10, 10, and 12 respectively; uropods with about eight or nine setæ, five on cephalic, 3-4 on lateral, and one on caudal aspect; glandulæ long, slender, subequal in length to adjacent setæ; spiracles not winged; length 18 mm.; width of head 1.8 mm.; on *Pteris aquilina*; Y-21.....*annulosus* Norton.
- 2(1) Head without blackish brown markings, uniformly pale brown.....3.
- 3(4) Trochanter distinctly shorter than femur; labial palpi with distal segment as long as the preceding segment; head uniformly pale; body and legs uniformly green without markings; annulation, 1, (3, 4, 5), (6, 7, 2); antennæ slender, 5, 1, (4, 3, 2); maxillary palpi, (2, 1), (4, 3), distal segment longer than that of labial palpi; labrum



and clypeus with four and three setae respectively on each side; larvapods with about 6-8 setae, 4-5 on cephalic, 2-3 on lateral aspect; glandubae subequal in length to adjacent setae; spiracles with faint brown wings; thoracic legs with trochanter, femur, and tibia with lengths to each other as 8, 13, and 15 respectively; length, 19 mm.; width of head, 1.6 mm.; on *Pteris aquilina*; Y-168-4.....*tacitus* Say.

- 4(3) Trochanter not distinctly shorter than femur; labial palpi with distal segment shorter than the preceding segment; head uniformly pale, rarely with a pair of faint spots on dorsal part of vertex; body uniformly green; legs distad of trochanter brownish; annulation, 1, (5, 4, 3), (2, 6, 7); antennae, slender, conical, (5, 1), 4, (2, 3); maxillary palpi, 2, (4, 1), 3, distal segment subequal to that of labial palpi; labrum and clypeus with four and three setae respectively on each side; thoracic legs with trochanter little shorter than femur, tibia usually almost as long as femur; length, 21-23 mm.; width of head, 1.8 mm.; on *Pteris aquilina*; Y-18-1, M-32 (in part), M-86. *politus* Provancher.

### SELANDRIA LEACH

Larvae comparatively small, length less than 24 mm., usually about 15 mm.; body slender, finely annulate; head pale; body green; tenth abdominal tergum unmarked; larvapods glabrous; legs very short, with tibia conspicuously reduced in size, femur distinctly dilated at distal end, bearing rudimentary tibia on dorsal margin; clypeus with two setae on each side; mandible with two setae; labrum with three setae on each side; glandubae very small; spiracles not winged.

*Selandria flavipes* Norton.—Legs with trochanter ring-like, femur dilated at distal end, with ventro-mesal projection only slightly narrower in diameter than trochanter; tibia very small, much smaller in diameter than femur, appearing as if surrounded by fleshy part of the latter, deep brown in color; trochanter, femur, and tibia with lengths to each other as 7, 11, and 6, respectively; annulation, 1, 4, 2, (3, 5, 6, 7); antennae slender, conical, 5, (1, 2, 4, 3); maxillary palpi, (4, 1, 2), 3; labial palpi with distal segment subequal in length to segment 1, longer than distal segment of maxillary palpi; length, 15 mm.; width of head 1.3 mm.; on *Pteris aquilina*: Y-168, M-70, C-S.f.

### SUBFAMILY DOLERINAE

Larvae (Fig. 10) moderately large, length, 15-25 mm.; body slender, cylindrical, tapering uniformly and gradually caudad, either uniformly greenish or brownish, or dorsum colored darker than venter, never with bright and distinct patterns; segmentation and annulation distinct; third abdominal segment with six annulets, annulets 2 and 4 on dorsum setiferous and with glandubae; larvapods on abdominal segments 2-8 and 10; thoracic legs well developed; head large, as wide as thorax or nearly so; vertical furrows distinct; antennae five-segmented, conical; labrum distinctly asymmetrical, dextral part larger than sinistral; head, legs, larvapods, tenth abdominal tergum, and sternum moderately setiferous; glandubae present; spiracles not winged; cuticle distinctly, uniformly, micro-

scopically verrucose on the dorsum and latus between spiracular lines; on monocotyledonous plants.

The Dolerinae is a well-defined subfamily with a distinct habitus and is closely allied to the Emphytinae and Selandriinae. The most important adult character for differentiating the group from other subfamilies of the generalized Tenthredinidae is the coalescence of the cells  $R_4$  and  $R_5$  due to the atrophy of the free part of the vein  $R_5$ . The subfamily contains two genera, the old genus *Dolerus* and the recently described genus *Loderus*. Leach separated, under the name of *Dosytheus*, all those species having certain antennal peculiarities and, according to Stephens, also having bright colors on the abdomen. This differentiation was considered invalid by Hartig and his view was endorsed by Norton and Cameron. Norton described a species under the name of *Dorytheus apricus* var. *albifrons* which is now placed in the genus *Loderus*. The monobasic genus *Pelmatopus* of Hartig, based on *P. minutus*, is now considered as congeneric with *Dolerus*. Since the larvae of *Loderus* are unknown, the genus *Dolerus* alone is considered here.

#### DOLERUS JURINE

Head viewed from cephalic aspect circular in contour in mature specimens, epicranium semiglobose, front distinctly flattened; mouthparts directed caudo-ventrad; antennaria never circular, with obtuse corners at the angles of their dorsal side; antennae with formula, 5, (3, 4, 2), 1, distal segment conical, apex less chitinized and obtusely rounded, never sharply pointed, segments 2-5 well chitinized, segment 1 narrow but distinctly larger in diameter than distal segments; front distinctly wider than high; labrum asymmetrical, dextral part always larger than sinistral or with pointed ventro-mesal angle; mandible very thick, large, dextral with four distadentes and one curved sharp proxadentis, sinistral with four distadentes and mesal surface deeply emarginate; parapharynx with apex dilated and chitinized; maxillary palpi, galea, lacinia, and labial palpi normal in structure and well chitinized; thoracic legs with femur often produced papilla-like on its disto-ventral angle, tibia long, cylindrical, tapering uniformly distad, distinctly longer than femur, tarsal claw rather slender and straight; abdominal segments with six annulets, typical formula, (1, 2), 3, 4, (5, 6),  $1=5+6$ ; spiracles on annulet 2; annulets 2 and 4 with conical glandubae and tiny cylindrical truncate setae with large calices; tenth abdominal tergum semiglobose, anal setae numerous; ventral glands never present.

The genus *Dolerus* is represented in North America by more than thirty species but none of them had been identified in the immature stages until the writer reared the adult of *D. similis* Nort. at Ithaca, N. Y. The

larvae of this genus are easily obtained and readily identified because of the marked asymmetry of the labrum.

The following key will serve to separate the species studied:

#### SPECIES OF DOLERUS

- 1(6) Head uniformly pale, creamy, or pale brown; body uniformly whitish or greenish, without distinct dorsal band. ....2.
- 2(3) Body with small black spots on each segment along supraspiracular and pedal lines; head pale brownish yellow; spots on ninth abdominal segment much smaller than preceding ones; length, 25 mm.; on wheat and grasses; Y-117-1-1, G-d-1. *Dolerus* sp. 1.
- 3(2) Body without small black spots on each segment along supraspiracular and pedal lines; head creamy; length less than 25 mm. ....4.
- 4(5) Distance between antennaria and mandibularia subequal to distance between antennaria and ocularium; length, 20 mm.; on *Carex trichocarpa*; Y-24-5-2, -145-1(?), -147. *Dolerus* sp. 2.
- 5(4) Distance between antennaria and mandibularia twice or more than twice the distance between antennaria and ocularium; length of prothoracic spiracles in relation to vertical diameter of antennaria variable; femur with or without disto-ventral projection; front with or without pale brown spot; length 18-20 mm.; on grasses, sedge, timothy; Y-29-11,-32-1, M-7, H,-41-1,-63,-225. ....*Dolerus* sp. 3.
- 6(1) Head spotted, banded, or distinctly brown, black, or purple; body uniformly longitudinally banded or striped on dorsum, especially along dorso-lateral lines, rarely uniformly whitish or greenish. ....7.
- 7(8) Head with a distinct blackish semicircular band extending from gena to gena dorsad of front and involving ocellaræ; body with a very fine brownish line along latero-dorsal lines, more distinct on caudal segments; thoracic legs uniformly pale; length, 15 mm.; on grasses; Y-41-1-1,-41-2,-41-3,-8.47(?) M-41,-235. ....*Dolerus* sp. 4.
- 8(7) Head without distinct blackish semicircular band, but with spots or dark-colored areas; thoracic legs with femur, tibia, and claws brown, not concolorous with coxa. .9.
- 9(12) Head pale brown, vertex with brown spots; body uniformly whitish or with light dorsal band. ....10.
- 10(11) Vertex with two small spots, one dorso-mesad of each vertical furrow, variable in size but never linear along the furrow; body uniformly whitish or creamy; length. 21 mm.; on *Carpinus* and *Pteris aquilina* (both doubtful); Y-74-1-1, M-82. ....*Dolerus* sp. 5.
- 11(10) Vertex with one minute spot at the origin of epicranial stem; light brown spot along epicranial suture to ocellaræ; body with dorsal band lighter on dorso-meson and darker on supraspiracular lines, more distinct on caudal segments; length, 15 mm.; on *Equisetum arvense*; Y-145-2. ....*Dolerus* sp. 6.
- 12(9) Head brownish with purplish or brownish markings on vertex, only rarely light brown or yellowish, then vertical furrows with brownish streaks; body with distinct dorsal band. ....13.
- 13(14) Head deep purplish black with following parts whitish: proximal half of epicranial stem, vertical furrows, vertex caudad of ocellaræ to the middle of epicranial stem very narrowly, epicranial arms, clypeus, and labrum; dorsal band lighter on dorso-meson; pedal lines with a row of grayish patches; legs with femora without disto-ventral projection; length, 19 mm.; on *Equisetum arvense*; Y-146-1-2. .*similis* Norton.
- 14(13) Head usually brownish or yellowish, vertex deeply brown, at least along vertical furrows; typically pale on vertex ventrad of vertical furrows and caudad of ocellaræ; front with or without brownish spot; tenth abdominal tergum on both sides usually



more brownish than on meson; legs with femora without disto-ventral projection; length, 20-23 mm.; on sedges; Y-28-1,-27-1-1,-30,-210-1-8.32 (?) -1-1, M-7,-8,-9,-35,-64,-193,G-d-3.....*Dolerus* sp. 7.

#### SUBFAMILY PHYLLOTOMINAE

Larvae (Fig. 11-12) small, length usually less than 15 mm.; body sub-cylindrical or depressed, without colored patterns; larvapods on abdominal segment with two or six annulets; antennae with 3-4 or 5 segments; thoracic legs with four segments, short, stubby, with or without tarsal claws.

The Phyllotominae can be divided into two distinct tribes on the basis of the larval characters. The tribes can be separated as follows:

Thoracic legs with tarsal claws; head normal in form, not depressed; third abdominal segment with six annulets; external feeders.....Phyllotomini.

Thoracic legs without tarsal claws; head depressed; third abdominal segment with two annulets; leaf-miners.....Phlebatrophini.

The Phyllotominae is a distinct group and includes four genera, *Phyllotoma*, *Caliroa*, *Endelomyia*, and *Phlebatrophia*. In the Nearctic region, the last three genera are represented by a limited number of species. MacGillivray considered this family as one of the five generalized sub-families of the Tenthredinidae, quite apart from the Fenusinae and Scolioneurinae, but Rohwer would associate them in his subfamily Mes-sinae while Konow would include Hoplocampinae and Phyllotominae in his tribe Hoplocampides. The subfamily is divisible into two distinct groups according to the characters of the larvae. The remarkable specialization of structures due to the leaf-mining habit of the larva in one genus where specialization has proceeded much further than in any of the other leaf-miners, makes the division of the subfamily into two tribes desirable.

#### TRIBE PHYLLOTOMINI

Body practically subcylindrical, thorax distinctly swollen, sometimes distinctly tadpole-like, tapering caudad; segmentation and annulation indistinct, fine, subequal in length; third abdominal segment with six annulets, annulets 2 and 4 microscopically and sparsely setiferous or minutely tuberculate; tenth abdominal tergum with or without tubercles; thoracic legs as long as head is wide, subequal in size, short, modified, with four segments, stubby, with distinct tarsal claws, coxa conical, femur cylindrical, as long as wide, tibia convex, wider than long, distal segment very minute, with sharp incurved claw; larvapods on abdominal segment 2-8 normal in form, glabrous, distal lobe with a minute point on its cephalo-ventral angle; ultimate segment with a pair of normal larvapods or without any; head small, normal, not depressed, sparsely setiferous, longer than



wide, slightly pointed at dorsal apex; mouth directed slightly ventro-caudad; antennae with four or five segments, slender, elongate, conical, or subconical; mouth-parts normal in form; spiracles with or without wings; ventral glands wanting; prothoracic glands sometimes present; glandubae present, conical, tuberculate or sessile; cuticle usually microscopically verrucose; larvae in life sometimes distinctly slimy; subgregarious; leaf-skeletonizers.

#### GENERA OF PHYLOTOMINI

Body without minute tubercles, tadpole-like, slimy; glandubae sessile. . . . . *Caliroa* Costa.

Body with minute tubercles, not tadpole-like, not slimy; glandubae conical, tuberculate.

*Endelomyia* Ashmead,

#### ENDELOMYIA ASHMEAD

Larvae small, length less than 15 mm., greenish yellow; body subcylindrical, apparently almost glabrous, not tadpole-like, thorax thickened, tapering caudad; third abdominal segment with six annulets, annulets 2 and 4 tuberculate; tenth abdominal tergum with eight to ten conical tubercles arranged approximately in three transverse rows; suranal and subanal lobes with several rather long stiff setae; thoracic legs with distinct tarsal claws; larvapods on ultimate segment normal in form, separated; antennae with five segments, slender, elongate-conical; mandibles with dentes; spiracles not winged; spiracles on sublateral lines; prothoracic glands wanting; glandubae conical, tuberculate; body not slimy.

*Endelomyia aethiops* Fabricius.—Length, 13 mm.; width of head, 1.2 mm.; head light brown; mouth-parts, labrum, and tarsal claws deep brown; body greenish yellow to yellowish white; tubercles concolorous with body; typical tubercular formula on prothorax: 3-6 on first annulet, 2-3 on prosubspiracular lobe, 2-5 on annulet 2; third abdominal segment with 2 and 3 tubercles on annulets 2 and 4 respectively, 1 on annulet 3 near the spiracle, 1 each on subspiracular and surpedal lobe; annulation, 1, 2, 3, 4, (5, 6); antennae, 1, (2, 3, 4), 5; maxillary palpi, (1, 2, 3), 4; labial palpi, 1, 2, or (1, 2); subgregarious; on Rosa; Y-2, M-127.

#### CALIROA COSTA

Larvae small, length 6-12 mm., whitish; body distinctly tadpole-like; thorax conspicuously swollen, rounded on dorsum and flattened on venter; tapering distinctly caudad; third abdominal segment with six indistinct annulets, annulets 2 and 4 with a few glandubae; tenth abdominal tergum without tubercles; suranal and subanal lobes often with a number of stiff rather long setae; thoracic legs with distinct tarsal claws; larvapods on ultimate segment obsolete, their position indicated by a small median swelling; antennae with four segments, rather thick, elongate, distal segment microscopic; mandibles with dentes; spiracles usually winged;

spiracular line abnormally low in position, coinciding with latero-ventral line; prothoracic glands present, large, triangular, fleshy, attached cephalomesad of prothoracic legs; glandubae sessile;

#### SPECIES OF CALIROA

- 1(2) Anal setae not all of same type and length, longer ones arising from minute but distinct tubercles, brown, apparently barbed, curved at tips, as long as labrum, ten to twelve in number, arranged in a transverse row on suranal and subanal lobe; spiracles distinctly winged, brown; clypeus light brown; head deep brown; thoracic legs and antennae deep brown; smaller setae on anal area normal in form, much shorter than the long barbed ones, scattered beyond the transverse rows; lengths of front, clypeus, labrum, and width of labrum to each other as 23, 10, 8 and 12 respectively; length of body, 11 mm.; width of head, 1 mm.; on cherry, plum, *Crataegus*; Y-209, M-260, -249, -115, C-551, -552. . . . . *cerasi* Linnaeus.
- 2(1) Anal setae all of same type and length, none arising from distinct tubercles and barbed, all of normal type, much shorter than labrum; spiracles usually not winged. 3.
- 3(8) Head blackish, deep brown, or brownish; legs brownish in part, not concolorous with body. . . . . 4.
- 4(7) Head blackish or dark brownish. . . . . 5.
- 5(6) Head black or dark brownish black; anal setae scattered, pale, subequal in length, about three-fifths as long as labrum; prothoracic legs distinctly lighter in color than other legs, which are brownish; spiracles of cephalic segments faintly winged; clypeus whitish; lengths of front, clypeus, labrum, and width of labrum to each other as 22, 9, 8, and 11, respectively; length of body, 10.5 mm.; width of head, 1 mm.; on oak; M-157, -200, -245, G-553c, Y-mck. . . . . *Caliroa* sp. 1.
- 6(5) Head deep brown; anal setae scattered, subequal in length; prothoracic legs higher in color than other legs; spiracles never winged; anal setae about one-third as long as labrum; clypeus pale brown; lengths of front, clypeus, labrum, and width of labrum to each other as 18, 10, 8, and 11 respectively; length of body 6 mm.; width of head, .9 mm.; on wild cherry; C. . . . . *obsoleta* Norton.
- 7(4) Head brownish or light brown; all legs pale brownish; anal setae scattered, subequal in length, about one-third as long as labrum; clypeus pale brown; lengths of front, clypeus, labrum, and width of labrum to each other as 10, 9, 7, and 11, respectively; length of body, 8 mm.; width of head 1 mm.; on white oak and *Crataegus*; C-7, M-230. . . . . *quercus-alba* Norton.
- 8(3) Head pale brown or whitish; legs whitish, concolorous with body; spiracles not winged; anal setae scattered, subequal in length, about three-fifths as long as labrum; lengths of front, clypeus, labrum, and width of labrum to each other as 21, 9, 7, and 10, respectively; length of body, 10.5 mm.; width of head, 1 mm.; Y-121, G-553c, M-143, -201, -231, -236-242. . . . . *quercus-coccinea* Dyar.

#### TRIBE PHLEBATROPHINI

Body viewed from the side distinctly depressed, venter flattened, thorax thickened, broadest on mesothorax, prothorax declivous cephalad, caudal segments distinctly tapering; segmentation and annulation distinct; third abdominal segment with two annulets, annulet 2 sparsely and inconspicuously setiferous; tenth abdominal tergum without tubercles; tenth sternum small; thoracic legs modified, fleshy, indistinctly four-segmented,

tapering to distal end, distal segment microscopic, mamma-like, without tarsal claw; larvapods vestigial, located on abdominal segments 2-8 and 10, anal larvapods united on the meson, forming a single sucker-like protuberance; head distinctly depressed, pointed, subtriangular in contour, partly overlapped by protruding prothorax; mouth directed cephalad; vertical furrows obsolete; antennae with 3-4 segments, segments 1 and 2 large and conical, segments 3 and 4 subcylindrical and much smaller and less in diameter than proximal segments; mouth-parts modified, mandibles slender, sharply pointed, without dentes, blade-like; labium flattened and large; spiracles not winged; ventral and prothoracic glands wanting; glandulae obsolete; body not slimy; leaf-miners.

#### PHLEBATROPHIA MACGILLIVRAY

Larvae very small, whitish; length less than 10 mm.; body distinctly depressed, tapering much caudad, broadest on mesothorax, prothorax declivous cephalad; lateral lobes somewhat prominent; tenth abdominal tergum convex, almost glabrous, about half as wide as mesothorax; suranal and subanal lobes semiglabrous; third abdominal segment with two annulets, caudal annulet about four times as long as the cephalic, microscopically and sparsely setiferous; thoracic legs fleshy, tarsal claws wanting; larvapods rudimentary; ocellaria protruding, located laterad of antennariae; epicranial suture in part obsolete; spiracles not winged; spiracular line normal in position; maxillary palpi with four segments, labial palpi with two segments; totiglossa roundly protruding; stipes elongate, subgalea long, slender, with distinct chitinized carinae; labrum flattened; mandibles slender, sharply pointed, without dentes, blade-like; leaf-miners.

*Phlebatrophia mathesoni* MacGillivray.—Length, 7 mm.; width of head, 1 mm.; mesothorax, 2.4 mm. wide; head light brown, mandibles and carinae of subgaleae deep brown; maxillary palpi typically 2, 1, 3, 4, distal segment very minute; antennae with proximal segment or segments larger in diameter and fleshy, conical, two distal segments together smaller and shorter than the other two segments, but longer than labial palpi; distal segment of labial palpus very minute; leaf-miners of birch; C and G.

#### SUBFAMILY TENTHREDININAE

Larvae (Fig. 13) of medium to rather large size; body cylindrical, slender, tapering uniformly and gradually caudad; segmentation and annulation distinct, fine; third abdominal segment with seven annulets, annulets 1, 3, and 5 setiferous and 3 and 5 with transverse row of glandulae; abdominal segments 2-8 and 10 with larvapods; antennae with five segments, slender, cylindro-conical; body uniformly greenish, with dark



dorsal band or with complicated color-patterns; tenth abdominal tergum convex, suranal or caudal protuberances wanting; ninth abdominal tergum with six annulets, annulet 6 as long as annulet 2; thoracic legs normal, well developed, femur with ventro-distal, conical membranous projection; clypeus with two setae on each side; labrum with 3-5 setae on each side, with or without a median longitudinal depression; maxillary palpi slender, normal; galea digit-like, large; lacinia flattened, with a row of 10-15 setae on the oblique, truncate cephalic margin; stipes with a sharp triangular cephalo-ventral projection; labial palpi long, slender, with segment 2 longer than segment 1; mandible with 1, 2, or 3-4 setae; head variously marked, distinctly and densely setiferous; spiracles on third annulet, not winged; larvapods glabrous; glandubae distinct, slender, elongate cylindro-conical, sometimes longer than adjacent setae; cuticle microscopically and densely spinulate; ventral glands wanting; larvae free leaf-feeders.

The Tenthredininae constitutes, according to MacGillivray, the second subfamily of the series of specialized Tenthredinidae. Rohwer (1911) would divide the subfamily into two tribes, Perineurini and Tenthredinini, using the position of the propodeal spiracles and shape of the cephalic margin of the scutellum as characters for differentiating them. In many cases the larvae resemble those of the Emphytinae.

#### GENERA OF TENTHREDININAE

- 1(4) Mandibles with more than one seta; labrum with median longitudinal depression; legs with dorsal aspect of femur usually less than twice as long as trochanter, but often subequal to it.....2.
- 2(3) Mandibles with two setae.....*Macrophya* Dahlbom.
- 3(2) Mandibles with four, occasionally three, setae.....*Tenthredo* Linnaeus.
- 4(1) Mandibles with a single seta; labrum without median longitudinal depression; legs with dorsal aspect of femur usually twice as long as trochanter.....5.
- 5(6) Body with complexly patterned markings on the dorsum; distal segment of maxillary palpi usually longer than that of labial palpi; head nearly black.. *Tenthredopsis* Costa.
- 6(5) Body without complexly patterned-markings on the dorsum; distal segment of maxillary palpi usually not longer than that of labial palpi; head pale or light brown  
*Neopus* MacGillivray

*Tenthredopsis semilutea* Norton.—Body on dorsum with complexly patterned purplish-black markings extending to suprspiracular lines; two lighter colored spots on dorso-meson, their apices directed cephalad, cephalic one much larger than caudal; large spot with caudal emargination on latus and contiguous to mesal triangles; subspiracular lobe with faint, minute spots; otherwise ventral half of body including legs and larvapods whitish; head purplish black excepting the following parts, which are white: genae including antennae and antennariae, lower fourth of front, vertex narrowly, laterad of vertical portion of epicranial arms, clypeus, labrum, and mouth-parts except tips of mandibles, which are black;



fronto-clypeal suture sometimes black; in young specimens, head grayish and body entirely whitish-green; in life head and body coated with a waxy bloom; annulation, (3, 5, 1), (2, 4), 6, 7; antennae, 5, 2, (1, 3, 4); maxillary palpi, (4, 2), 3, 1; labial palpi with distal segment twice as long as the preceding segment, but subequal in length to or shorter than distal segment of maxillary palpi; labrum usually with three setae on each side and without median longitudinal depression; mandible with one seta; legs with trochanter one-half as long as tibia, femur slightly longer than tibia; glandubae half as long as adjacent setae; length, 18 mm.; width of head, 1.8 mm.; on *Thalictrum polygamum*; Y-8,-92-1-1.

*Neopus 14-punctatus* Norton.—Head pale creamy-white with brown spots on dorso-meson of vertex, caudad of ocellaræ, and on front, frontal spots much darker; body whitish green, dorsum with a grayish shade, bordered along supraspiracular lines with narrow grayish bands, dorso-meson, especially on thorax, with fine double bands; venter including legs and larvapods whitish; annulation, (1, 5, 3), (2, 4, 6, 7); antennae, (5, 1), 2, (3, 1); maxillary palpi, 4, 2, (3, 1); labial palpi with distal segment one-fourth longer than preceding segment, but subequal to distal segment of maxillary palpi; labrum with three setae on each side, median longitudinal depression wanting; mandible with single seta; legs with trochanter nearly one-half as long as femur, tibia equal in length to femur; glandubae more than half the length of adjacent setae; length of body, 18 mm.; width of head, 1.8 mm.; on *Podophyllum peltatum*: Y-205-1-1.

*Tenthredo bilineata* MacGillivray.—Head whitish green with vertex brown dorsad of genae except narrow line along epicranial stem, vertical furrows, and caudad and dorsad of ocellaria; body on dorsum with series of triangular brownish markings; triangle with apex directed cephalad and with minute deep brown spot at each basal angle, the triangle divided on meson by a faint light line; supraspiracular line with light brownish indefinite band; venter including legs and larvapods whitish; annulation, (3, 1, 5), (7, 6, 2, 4); antennae, 5, (1, 2, 3, 4); maxillary palpi, (4, 2), 1, 3; labial palpi with distal segment nearly twice as long as the preceding segment and shorter than distal segment of maxillary palpi; labrum with five setae on each side and with median longitudinal depression; mandibles with four setae; legs with trochanter nearly as long as femur, tibia longer than femur; glandubae conical, large, subequal in length to adjacent setae; length of body, 21 mm.; width of head, 2 mm.; on *Geranium maculatum*: Y-175-2.

#### MACROPHYA DAHLBOM

Body usually whitish green, on dorsum with or without grayish band, latus sometimes with small black spots; head usually marked on vertex; antennae with segment 1 or 2 longest or all segments subequal in length;

maxillary palpi usually with segments 2 and 4 subequal in length; mandible with two setae; labrum with three setae on each side, with median longitudinal depression; trochanter distinctly shorter than femur; head and body in life usually coated with a thin whitish waxy bloom; dorsal vessel usually showing thru cuticle as a dark fine line; setae microscopic; glandubae shorter or longer than adjacent setae; length, 16-21 mm.

#### SPECIES OF MACROPHYA

- 1(4) Head pale brown, with or without a minute brown spot at the caudal end of epicranial stem; body on dorsum with light or pale grayish band, darker along supraspiracular lines, band sometimes obsolete; venter whitish, including legs and larvapods; tenth abdominal segments unmarked; labial palpi with distal segment twice as long as the preceding segment; glandubae very small, shorter than adjacent setae; setae microscopic; head and body coated with thin waxy bloom; on *Prunus serotina*; subgregarious. . . . . 2.  
*ficta* MacGillivray.
- 2(3) Larger species, length, 20 mm.; width of head, 1.8 mm.; annulation, (1, 5), 3, (4, 6, 7), 2; antennae, (2, 1), (3, 4, 5); maxillary palpi, 2, (1, 3, 4); Y-126,-126-3-C-1. . . . .  
*fistula* MacGillivray.
- 3(2) Smaller species, length, 16 mm.; width of head, 1.8 mm.; annulation, (5, 1, 3), 4, 6, 2, 7; antennae, 2, (5, 1, 4), 3; maxillary palpi, (2, 4), (3, 1); Y-59-3-1,-59-4-1. . . . .  
*fistula* MacGillivray.
- 4(1) Head with a large blackish spot on dorsal part of vertex, often with black spots caudad of ocellaræ; body with or without distinct grayish dorsal band, on latius with rows of black or yellowish spots; venter usually whitish; pedal line sometimes with fine gray markings. . . . . 5.
- 5(8) Body entirely whitish; head on vertex usually with a dorsal spot not expanding distad; without spots caudad of ocellaræ. . . . . 6.
- 6(7) Body with a row of small black spots along supraspiracular lines, two spots to each segment, cephalic spot larger than caudal; tenth abdominal tergum unmarked; annulation, (1, 3, 5) (4, 7), (6, 2); antennae, (4, 1), 2, 3; legs with femur more than twice as long as trochanter, tibia shorter than femur, coxa with grayish marking; glandubae longer than adjacent setae; length of body, 22 mm.; width of head, 2.3 mm.; on *Sambucus*; Y-8.11,-11. . . . . *tibialis* Norton.
- 7(6) Body without a row of small black spots along supraspiracular lines, but with yellowish spots on latius instead, which are obsolete in alcoholic specimens; annulation, (3, 5, 1), (2, 7, 4, 6); antennae, 1, (2, 3, 4, 5); maxillary palpi, (4, 2), (1, 3); labial palpi with distal segment only one-fourth longer than the preceding segments; legs with trochanter slightly shorter than tibia, femur slightly longer than tibia; length of body, 22 mm.; width of head, 2.2 mm.; on *Sambucus racemosa*; Y-8.11-2(P)-3. . . . . *epinota* Say.
- 8(5) Body not entirely whitish, dorsum with dark dorsal band; latius with one or more rows of distinct black spots; head on vertex with a dorsal spot expanding distad, broadly T-shaped, caudad of ocellaræ with spots; tenth abdominal segment with a minute black spot on caudo-meson; venter lighter in color. . . . . 9.
- 9(10) Body on latius with grayish band darker in color than dorsal band and with only one row of distinct black spots; supraspiracular lines with a row of distinct spots; dorso-lateral lines with a row of smaller, inconspicuous spots; subspiracular line with very faint grayish spots, nearly obsolete; pedal lines with grayish linear markings; annulation, 1, (3, 5), (7, 2, 4), 6; antennae, (1, 2, 3, 4, 5); maxillary palpi, (2, 4), 1, 3; labial palpi with distal segment not quite twice as long as the preceding segment;

legs with femur twice as long as trochanter and slightly longer than tibia; length of body, 19 mm.; width of head, 2 mm.; on *Aster prenanthoides*; Y-8, 81(?).....

*lineata* Norton.

- 10(9) Body on latus with grayish band lighter in color than grayish-purple dorsal band and with three rows of distinct black spots; dorso-lateral and supraspiracular lines with rows of small spots, two spots to each segment, with caudal spot much smaller and sometimes nearly obsolete; spots on supraspiracular line largest; pedal line with a row of spots, two to each segment, with cephalic spots smaller than caudal; head with black spots on vertex large, sometimes coalesced, covering entire vertex except genae and vertical furrows; front with faint gray spot; annulation, (3, 5, 1), (7, 2, 4, 6); antennae, 2, (1, 5), (3, 4); maxillary palpi, (4, 2), (1, 3); labial palpi with distal segment not quite twice as long as the preceding segment; legs with trochanter more than one-half as long as tibia, femur equal in length to tibia; length of body, 21.5 mm.; width of head, 2.1 mm.; on *Solidago juncea* and *Rudbeckia laciniata*; Y-160-2, -160-1.....*pulchella* Klug.

#### SUBFAMILY CIMBICINAE

Body cylindrical (Fig. 14), tapering uniformly caudad, apparently glabrous, prothorax narrowed; segmentation indistinct; annulation fine, 7, (2, 3, 4), (1, 5, 6), annulets 2, 4, and 7 microscopically setiferous; thoracic legs normal in form, with five segments, femur slightly longer than tibia; larvapods on abdominal segments 2-8 and 10, divided into two unequal lobes on the distal surface, few setae on the dorso-caudal aspect, and none on the cephalic aspect as viewed from side; tenth abdominal tergum without suranal protuberances; suranal and subanal lobes with several short setae; head large, rather thickly setiferous, normal in form; labrum subdivided by diverging depression into median lobe and two lateral lobes, sometimes asymmetrical; antennae with a single segment, button-like but chitinized; ventral glands wanting; glandubae microscopic or minute and stalked, sometimes distinct conical tubercles; spiracles distinctly winged; conspicuous spiracular glands located dorsad of each spiracle of abdominal segments 2-8; cuticle microscopically and densely spinulate or verrucose; mouth-parts normal in form, maxillary and labial palpi rather slender, galea very thick, curved mesad at distal end, sericos large, distinctly chitinized, pear-shaped, U-shaped, or V-shaped; stipes with a distinct triangular projection on the dorsal or cephalic margin; body covered with waxy bloom in life; larvae ejecting yellowish fluid from spiracular glands when disturbed; free leaf-feeders, sometimes semigregarious.

The Cimbicinae is a small compact subfamily consisting of few genera and a limited number of species in the Nearctic region. Systematists are in accord in the general conception of the group, but Konow includes the Perginae in his subfamily Cimbicini. *Cimbex americana*, with its several varieties, is a well-known representative of this subfamily.



## GENERA OF CIMBICINAE

- 1(4) Body in general whitish, without minute colored spots.....2.  
 2(3) Dorsum of body with a black median stripe.....*Cimbex* Olivier.  
 3(2) Dorsum of body without a black median stripe.....*Trichiosoma* Leach.  
 4(1) Body in general not whitish, but with minute colored spots.....*Abia* Leach.

## CIMBEX OLIVIER

Larvae very large, distinctly robust, largest of all saw-fly larvae, 40–50 mm. in length; body whitish with a distinct dorso-mesal black line; labrum distinctly asymmetrical, dextral portion larger than sinistral, median cephalic or ventral emargination distinct and deep; body with distinct minute warts or conical glandubae, cuticle microscopically verrucose; spiracular glands semicircular; sericos of labium pear-shaped with its narrow neck directed dorsad or cephalad; lateral lobes small but prominent with several conical tubercles; maxillary palpi, 2, 4, 3, 1; labial palpi, 1, 2; antennae mound-like, wider than high

*Cimbex americana* Leach.—Length, 50 mm.; head, 5 mm. wide; head white, creamy, microscopically brownish verrucose; black median stripe on dorsum extending from prothorax to the middle of eighth abdominal segment; conical tubercles or glandubae on sublateral lobes larger than elsewhere and 4–7 in number; larvae solitary; on willow, elm, poplar, maple, alder, linden, etc.; Y-68, -8, -182, M-99.

## TRICHIOSOMA LEACH

Larvae very large, somewhat slender, entirely white; labrum slightly asymmetrical, right side larger than sinistral, median ventral emargination deep, but not reaching the median lobe; body not warty; glandubae microscopic, stalked, arising from very low swellings; cuticle microscopically verrucose; spiracular glands semicircular; sericos of labium U-shaped, narrower on dorsal or cephalic end; lateral lobes not prominent, without conical tubercles; maxillary palpi 2, 4, 3, 1; labial palpi, 1, 2; antennae conical, longer than wide.

*Trichiosoma* sp.—Length, 38 mm.; width of head, 4 mm.; head creamy white, body whitish; solitary; on willow, poplar, alder, wild cherry; M-78, -44.

## ABIA LEACH

Larvae large, rather plump, greenish or grayish green with minute yellowish or blackish spots; labrum symmetrical, median ventral emargination only slightly indicated, broad; body without warts or tubercles; cuticle microscopically and densely spinulate; glandubae stalked and minute, not arising from swellings; spiracular glands semicircular; sericos of labium V-shaped, widest at dorsal or cephalic end; sublateral lobes



inconspicuous, with several glandubae; maxillary palpi, (4, 2) 3, 1; labial palpi with segments subequal; antennae conical, usually as wide as long.

#### SPECIES OF ABIA

- 1(2) Body with a broad dorso-mesal yellowish stripe between subdorsal lines; dorsum above supraspiracular lines shaded brownish gray; head brownish gray except front, genae, clypeus, and labrum which are lighter; ocellaræ white; body dorsad of supraspiracular lines shaded grayish or brownish, venter pale whitish-green; dorsum between subdorsal lines yellowish white; body with four rows of minute black spots; middorsal row with a large spot on annulet 7 and a smaller spot on annulets 2 and 4; subdorsal row with a large spot on annulet 7, with a bright yellow spot between two black spots mentioned above; supraspiracular row with a spot on annulets 2 and 4 and a very small spot on annulet 7; subspiracular row with a spot at the ventral ends of annulets 3 and 4; a yellow spot caudad of each spiracle; length, 26 mm.; width of head, 2.7 mm.; on honeysuckle; semigregarious; Y-8.13.....  
*americana* Cresson.
- 2(1) Body with a broad dorso-mesal yellowish stripe between subdorsal lines; dorsum above supraspiracular lines not shaded brownish-gray, but body generally greenish... 3.
- 3(4) Pedal line without distinct more or less continuous smoky brownish gray band; black spots directly ventrad of spiracles never present; second annulet without minute but distinct spots dorsad of lateral large spots; head grayish brown except front, genae, and clypeus, labrum lighter; ocellaræ white; body entirely grayish green, dorsum between subdorsal lines concolorous with other parts, the dorso-meson with a narrow yellowish line; five rows of minute black spots: meso-dorsal row with a larger spot on annulet 7 and a smaller spot on annulets 2 and 4; subdorsal row with a larger spot on annulet 7 and very minute and often obscure spot on annulet 2, and larger, distinct, often subdivided, spot on annulet 4, the latter two nearer to meson than the regular subdorsal spots; lateral row with a large spot between annulets 2 and 3; supraspiracular row with a smaller spot on annulets 4 and 7; subspiracular with a larger spot at the ventral end of annulets 3 and 4; a bright yellow spot between mesal and subdorsal black spots on annulet 7; length, 28 mm.; width of head, 2.8 mm.; on *Triosteum aurantiacum*; Y-8.13-2, M-196.....*inflata* Norton.
- 4(3) Pedal line with distinct, more or less continuous smoky brownish gray band; black spots directly ventrad of spiracles always present, at least on majority of segments; one or two minute black spots on second annulet dorsad of large lateral spots always present; length, 30 mm.; width of head, 2.9 mm.; on honeysuckle; Y-104, G-583, both from Urbana, Ill.; larvae resemble *A. inflata* in markings and general appearance but differ as above.....*Abia* sp. 1.

#### SUBFAMILY HOPLOCAMPINAE

Larvae (Fig. 15) small; body cylindrical, slender; segmentation and annulation sometimes obsolete; third abdominal segment with four or five annulets, annulets 2 and 3 or 2 and 4 setiferous or all annulets glabrous; larvopods present on abdominal segments 2-7 and 10, glabrous or setiferous, sometimes very rudimentary; ventral glands usually present on the meson of abdominal segments 1-7; body greenish or yellowish, striped or spotted or without any markings; tenth abdominal tergum with or without suranal protuberances, if present, often more than two in number; antennae

conical, with five segments, or flattened, with four, sometimes apparently with three; larvae free leaf-feeders and borers in fruits or petioles of leaves.

The Hoplocampinae as defined by MacGillivray contains at present five genera, *Marlattia*, *Hoplocampa*, *MacGillivrayella*, *Hemichroa*, and *Craterocercus*, and represents, together with *Dineurinae*, a series in which the anal veins have been modified before the loss of the radial cross-vein. Formerly Rohwer (1910, 1911a, 1913b) considered *Hoplocampa* and *MacGillivrayella* as constituting a subfamily Hoplocampinae but later (1918c) he abandoned this idea and united these genera with six other genera and subgenera to form the tribe Hemichroini of his subfamily Nematinae, as others have done. With the exception of two genera, *Platycampus* and *Anoplonyx*, Rohwer's tribe Hemichroini becomes coextensive with our Hoplocampinae. Cameron (1883) considered this subfamily as forming "a connecting link between the Selandrides and Nematides." There are reasons for indicating a close relation between this subfamily and Nematinae. A study of the larvae confirms the contention of Rohwer (1918c) that the grouping of *Caliroa* and *Phyllotoma* with the Hoplocampinae, as was done by Konow and Enslin, is untenable.

It must be stated here that since only three genera, each represented by a single species, were available for this study, the preceding definition of the subfamily is necessarily incomplete.

#### GENERA OF HOPLOCAMPINAE

- |      |  |                            |
|------|--|----------------------------|
| 1(2) | Tenth abdominal tergum without caudal protuberances.....   | <i>Marlattia</i> Ashmead.  |
| 2(1) | Tenth abdominal tergum with caudal protuberances.....  | 3.                         |
| 3(4) | Caudal protuberances more than two in number; larvapoas well developed; third abdominal segment with five annulets; free leaf-feeders.....                                 | <i>Hemichroa</i> Stephens. |
| 4(3) | Caudal protuberances two in number on caudal projection; larvapoas rudimentary; third abdominal segment with four annulets; leaf-petiole borer. <i>Caulocampus</i> Rohwer. |                            |

#### HEMICHROA STEPHENS

Larvae small, greenish; length less than 18 mm.; body slender, tapering uniformly caudad; third abdominal segment with five annulets 2 and 4 setiferous; tenth abdominal tergum with several conical caudal protuberances on its caudal margin; antennae distinctly conical, with five segments, as long as the longest diameter of antennaria; antennal segment 1 crescentic, dorsal in position, extending nearly the entire length of antennaria, segment 2 complete or incomplete, reduced to mere line on cephalic aspect, segments 3 and 4 ring-like tho reduced in length on cephalic portion, segment 5 conical or peg-like, bluntly pointed at apex; thoracic legs with tibia subequal in length to femur; larvapoas glabrous; spiracles faintly winged; glandubae distinct and large; larvae free leaf-feeders.

*Hemichroa dyari* Rohwer.—Larvae yellowish green; length, 16 mm.; head blackish; body with blackish dorso-lateral lines and interrupted

blackish lines on subspiracular and pedal lines; tenth abdominal tergum with six to seven conical protuberances, suffused with brown; surpedal and subspiracular lobes with two setae and two glandubae; glandubae with diameter twice that of anal setae; annulation, (1, 2, 4) 3, 5; on alder; Y-39-1-1, -8.73 (?) -1, -8.73(?) -2, C-8.

#### MARLATTIA ASHMEAD

Larvae comparatively very small, greenish, with or without stripes or spots; body cylindrical, tapering caudad; third abdominal segment with five annulets, annulets apparently glabrous; tenth abdominal segment without caudal protuberances; antennae with four segments, flattened; segment 1 small, incomplete; segments 2 and 3 complete but reduced to narrow line on cephalic aspect; segment 4 minute, mamma-like; head sparsely setiferous, setae increasing in length on the lower portion; thoracic legs normal in form, tibia subequal in length to femur; larvapods with a few setae; spiracles minute, unwinged; glandubae microscopic.

*Marlattia laricis* Marlatt.—Head pale yellowish, body greenish with faint subdorsal lines; third abdominal segment with five annulets, (1, 2) 4, 3, 5; larvapods with three setae; suranal lobe with a few setae on caudo-ventral aspect; small larvae, length, 10 mm.; M-57.

#### CAULOCAMPUS ROHWER

Larvae very small; length less than 10 mm.; body subcylindrical, tapering at prothorax, constricted suddenly on the ultimate segment, not spotted or striped, but whitish, sparsely and microscopically setiferous; third abdominal segment with four annulets, annulets 2 and 3 with very minute setae; thoracic legs minute, with five segments, tibia longer than femur; abdominal segments 2-7 with rudimentary larvapods represented by spinulate swellings; tenth abdominal tergum much smaller in diameter than preceding segments, strongly converging caudad, caudal margin produced and chitinized, a pair of minute brownish caudal protuberances on the caudal margin of the projection; head small, sparsely and minutely setiferous; ocellariae represented by pigmented spots, distinct, ring-like, ocellaria wanting; antennae apparently with three segments, conical, segments 1 and 2 incomplete, segment 3 slender, peg-like; mouth-parts normal and conspicuous tho small; spiracles not winged; glandubae obsolete; in young specimens dorsum of abdominal segments 1-7, with a pair of protuberances on annulet 2; larvae borers in leaf-petiole.

This genus is monotypic and unique in the reduction of larvapods and ocellariae and in the possession of modified caudal projection on the ultimate segment with rudimentary caudal protuberances. In this last



character the larvae of this genus resemble those of certain species of *Pontania*. The modifications of the body are undoubtedly correlated with the boring habit of the larvae. MacGillivray still considers this genus as without question belonging to the Cladiinae, but Rohwer regards it as belonging to his tribe Hemichroini. It is dealt with here under the Hoplocampinae because the larvae more closely resemble larvae of this subfamily than they do those of the Cladiinae.

*Caulocampus acericaulis* MacGillivray.—Length, 8 mm.; width of head, .8 mm.; head light brown, body straw-yellow; resembles larvae of weevils in general appearance; mouth-parts normal in form; in young specimens head yellowish and body whitish; annulation, 2, 1, 3, 4; maxillary palpi, 3, 2, 1, 4, segments brown, slender; galea digit-like, very small; thoracic legs with very small tibiae, tibia subequal in length to maxillary palpus; tenth abdominal tergum with many minute setae evenly and promiscuously scattered, not concentrated on subanal lobe; larvae bore into the petioles of maple-leaves; Y (generosity of Dr. W. E. Britton, New Haven, Conn.).

#### SUBFAMILY DINEURINAE

Larvae small; body subcylindrical, flattened on venter or cylindrical, usually tapering toward the caudal end, greenish or yellowish, often with dorsum darker, never with bright-colored markings; glabrous or setiferous; head small, light greenish or yellowish, never with distinct markings; ocellaræ blackish; mouth-parts usually brownish; thorax wider than the remainder of body, thoracic legs well-developed, caudal pairs larger than the cephalic, directed laterad; segmentation distinct; annulation indistinct; larvopods on abdominal segments 2-7 and 10, sometimes rudimentary; intersegmental coria often distinct and whitish; larvae feed on under side or upper side of leaves, eating the parenchymatous layers only or feeding on edges of leaves or mining in the leaves; ultimate stage glabrous and yellowish; pupation in single-layered parchment-like cocoons in the ground; some species with nauseating odor.

The Dineurinae as limited by MacGillivray contains three genera, *Dineura*, *Mesoneura*, and *Pseudodineura*, and includes not over twenty-five species, which are mostly distributed in Europe and North America. This subfamily resembles in wing-type the Hoplocampinae. Systematists do not agree in the exact position of the small European genus *Pseudodineura*. Konow would place *Dineura* in his tribe Nematides but both *Mesoneura* and *Pseudodineura* in his tribe Blennocampides. Rohwer, on the other hand, would associate *Dineura* and *Mesoneura* in his tribe Nematini, and is not quite certain whether *Pseudodineura* also belongs to this tribe or not. Cameron, who described the larva of *Pseudodineura parvulus* under the name of *Dineura despecta*, altho aware of the differences



between this species and its allies and other species of *Dineura*, hesitated to agree with Thompson in associating it with *Blennocampa*. The venation certainly indicates close relationship between *Dineura* and *Pseudodineura*. The latter is characterized in its larval stages by the leaf-mining habit and structural modifications due to this mode of life, altho apparently these do not constitute very striking distinctions if one may judge from published records. Since previous authors failed to study the structures of the head more carefully, and since these are of great taxonomic importance, and also on account of the discrepancy between the larval habits of the three genera in question, it is impossible to pass judgment on their affinity until more is known with regard to their larval structures and habits, particularly in the case of *Pseudodineura*.

The life history of the subfamily has been recorded by Girard, Cameron, and Brischke and Zaddach. The larvae of the American species are unknown, and as none of the European species have been available for study the definition of the *Dineurinae* here given is tentative, and is based on descriptions and figures published by Cameron (1882) and by Brischke and Zaddach (1883).

#### SUBFAMILY CLADIINAE

Larvae (Fig. 16) of small to medium size; body rather flattened, wider than high, slightly tapering caudad, conspicuously hairy, greenish or with segmentally arranged spots on dorsum darkly shaded; segmentation and annulation usually distinct; third abdominal segment with four annulets, annulets 1, 2, and 3 setiferous, setae, especially on annulets 2 and 3, arising from wart-like tubercles, long, often curved, always microscopically barbed, never branched, some of the setae distinctly longer than others; annulet 4 narrow and glabrous; larvapods present on abdominal segments 2-7 and 10 well developed, long, distal portion often dilated, appearing as if subdivided, often curved mesad, always with few setae; ventral glands small but always present on abdominal segments 1-7; tenth abdominal tergum without caudal protuberances but with many setae of varying length; thoracic legs spreading flat laterad; femur with a ventro-distal projection, subequal in length to tibia; antennae with four segments, subconical, large; segment 1 complete or incomplete, segment 2 complete, thicker, dorsal or caudo-dorsal portion with clear spaces, segment 3 smaller and narrower than segment 2, segment 4 minute, conical; spiracles never winged; glandulae small or obsolete; sericos usually very wide, occupying nearly four-fifths of the width of the totiglossa; larvae external leaf-feeders.

The Cladiinae is a small subfamily and according to MacGillivray consists of six genera; *Anoplonyx*, *Platycampus*, *Priophorus*, *Cladius*, and *Trichiocampus*. The first three genera are placed in the tribe *Hemichroini* of his subfamily *Nematinae* by Rohwer (1911, 1918), who states that

"the characters of both the adult and the larva point out subfamily difference between *Caulocampus* and *Priophorus*" and that the former superficially resembles *Hoplocampa* in all stages but is really related to *Craterocerus*. The difference of opinion is due to the different value placed by these two writers on the presence or absence of the radial cross-vein in differentiating the subfamilies. The genus *Caulocampus* has been discussed in connection with the *Hoplocampinae* because the larvae of this genus are very different from those of the *Cladiinae* both morphologically and biologically and because they are more naturally associated with the larvae of the *Hoplocampinae*. *Anoplonyx* is represented in the Nearctic region by a single species. *Platycampus* includes four American species, two of which have been recognized in the immature stages. *P. americana* feeds on *Populus* and *P. juniperi* on juniper. None of these larvae have been examined.

#### GENERA OF CLADIINAE

- 1(2) Body spotted, with a row of blackish or brownish spots on subdorsal, supraspiracular or subspiracular lines; setae usually recurved exceedingly long, longest ones longer than one-half the height of the head; annulet 1 usually with one seta on each side of meson.....*Trichiocampus* Hartig.
- 2(1) Body never spotted; setae usually straight, long, but the longest ones never distinctly longer than half the height of the head; annulet 1 always with more than one seta on each side of meson, usually with four to six setae.....3.
- 3(4) Head with spots, usually with blackish patches on dorso-meson of vertex and caudad of each ocellara; body dorsad of spiracular lines usually shaded darker than the venter; body sometimes pinkish; postsupraspiracular tubercles usually with three setae, never with more than four.....*Priophorus* Dahlbom.
- 4(3) Head never with spots, usually uniformly greenish; body dorsad of spiracular lines never shaded darker but concolorous with venter; body never pinkish but greenish yellow or whitish; postsupraspiracular tubercles usually with six setae, never with less than four.....*Cladius* Rossi.

#### TRICHIOCAMPUS HARTIG

Larvae small to moderately large, length from 10 to 25 mm., distinctly hairy, with segmentally arranged spots; body with a longitudinal row of blackish or brownish spots along subdorsal, supraspiracular, or subspiracular lines; annulet 4 shortest, annulet 1 usually with one and sometimes two setae on each half of body, annulet 2 with tubercles bearing 2-5 setae, annulet 3 with three warts, two dorsal ones bearing 4-5 setae and ventral one with 6-9 setae, postspiracular tubercle usually with two setae, subspiracular lobe with 8-9 setae, surpedal lobe with 6-10 setae; setae usually recurved, variable in length, longest setae nearly subequal in length to the height of head; warts or tubercles with setae of varying length, those on annulet 1 among the shortest.

## SPECIES OF TRICHIOCAMPUS

- 1(2) Body with three pairs of longitudinal rows of blackish or brownish segmentally arranged spots along subdorsal, supraspiracular, and subspiracular lines; tenth abdominal tergum not entirely black but white except a pair of minute spots; head light brown with brownish spots, with following parts dark brown: dorso-meson of vertex, dorsal two-thirds of front, and vertex dorso-caudad of each ocellara including gena; preclypeus whitish, other parts pale, including occiput between vertical furrows; a row of brownish spots from mesothoracic to ultimate segment along each side of dorso-meson; a row of larger spots along supraspiracular line from prothoracic to penultimate segments; another row of much smaller spots along subspiracular lines from mesothoracic to eighth abdominal segment; mesothoracic and metathoracic subspiracular spots more than twice as large as supraspiracular spots of same segments; the former with circular white areas around the proximal end of setae; prothoracic supraspiracular spots small and indistinct; third abdominal segment with following setal map: 1, 3, 5, 1, 2, 5, 4, 8, 9-10, 8-9; tenth abdominal tergum white, except a pair of minute spots; subdorsal spots not involving tubercles 2 and 3; supraspiracular spot involving tubercles 4 and 5; subspiracular spot on caudal half of subspiracular tubercle; maxillary palpi (2, 3), 1, 4; head in younger specimens blackish except near the mouth; body without spots; in older specimens, supraspiracular spots appear first, then subspiracular, beginning with caudal segments, setae on tubercles sometimes one or two less than in mature specimens; on *Populus*; length of body, 12 mm.; width of head, 1.5-1.6 mm.; G-Onekama and Orono on oak, length of body, 13 mm.; width of head, 1.7 mm., M-207. (The latter resembles the former so closely and indistinguishably, altho its setae may be slightly fewer in number, that they are considered as identical.).....*paetulus* MacGillivray.
- 2(1) Body with two pairs of longitudinal rows of blackish or brownish segmentally arranged spots along supraspiracular and subspiracular lines; tenth abdominal tergum entirely black; head blackish, with paler areas.....3.
- 3(4) Mesothoracic supraspiracular spots subequal in size to subspiracular spots; supraspiracular spots of abdominal segments not involving postsupraspiracular tubercles; prothoracic supraspiracular spots minute and indistinct; preclypeus, labrum, and genae blackish; metathoracic subspiracular spots with minute but distinct circular whitish areas around proximal end of setae; head blackish, paler along vertical furrows, epicranial arms, and postclypeus; body with a row of blackish spots from mesothoracic to penultimate segment along supraspiracular and subspiracular lines; tenth abdominal tergum black; third abdominal segment with the following setal map: 1, 3, 3, 0, 2, 4, 4, 5-6, 8-9, 6-8; subspiracular spot involving few setae directly ventrad of spiracles; head in younger specimens entirely blackish and spots on subspiracular lines wanting; maxillary palpi, (2, 3), 1, 4; length of body, 18 mm.; width of head, 1.3 mm.; on *Salix*; Y-151-1-1, -151-1-3; M-100, -261. (The specimens in the Maine collection are practically identical with my specimens except in the number of setae on subspiracular and surpedal lobes, which may exceed the number given by one or two).....*patchiae* MacGillivray.
- 4(3) Mesothoracic supraspiracular spots not subequal to but distinctly larger, twice or more, than subspiracular spots; supraspiracular spots of abdominal segments involving postsupraspiracular tubercles; prothoracic supraspiracular spots large and distinct; preclypeus, labrum, and genae not blackish but pale brown; metathoracic subspiracular spots without minute but distinct whitish circular areas around the proximal end of setae; head black, paler along vertical furrows, epicranial arms, clypeus, labrum, and genae; body with a row of blackish or brownish spots from prothorax to penultimate segment along supraspiracular and subspiracular lines:



tenth abdominal tergum black; third abdominal segment with the following setal map: 2, 2, 3, 1, 2, 4, 4-5, 7-8, 8-9, 9-10; mesothoracic supraspiracular spot more than twice as large as subspiracular spot; prothoracic supraspiracular spots moderately large and distinct; subspiracular spot involving few setae in caudal portion of subspiracular tubercle; mesothoracic and metathoracic subspiracular spots without circular whitish areas around the proximal end of setae; maxillary palpi usually 3, 2, 1, 4; head in young specimens pale brownish, with a row of very small supraspiracular spots; head in older larvae blackish, body spotted like mature specimens but spots smaller; on *Populus*; length of body, 21-23 mm.; width of head, 2-2.1 mm.; Y-172-1-1.

*Trichiocampus* sp. 1.

### PRIOPHORUS DAHLBOM

Larvae small, hairy; length less than 17 mm.; body with dorsal half, at least in part, usually with grayish or olivaceous shade; never with spots; annulet 1 with a transverse row of several setae; annulet 2 with two warts, each bearing 4-5 setae; annulet 3 with three warts, dorsal two bearing 5-6 setae each, ventral with 8-10 setae; postsupraspiracular wart usually with three setae; subspiracular lobe with 12-15 setae and surpedal lobe with 6-9; setae usually more or less straight, usually of two different lengths, longer ones usually less than one-half the height of the head; warts bearing setae of two varying lengths, those on annulet 4 being among the shortest setae.

### SPECIES OF PRIOPHORUS

- 1(2) Front with a distinct blackish or fuscous spot; vertex with a dorso-mesal fuscous spot occupying nearly the entire space between vertical furrows; body never pinkish but whitish; head caudad of ocellaræ fuscous; body dorsad of spiracular lines from mesothorax to penultimate segment olivaceous or grayish, color becoming dilute on caudal segments; third abdominal segment with following setal map: 4-5, 4, 5, 1, 3, 6, 8, 12, 13, 8-9; maxillary palpi 2, (3, 4), 1; in younger specimens dorsal grayish shade confined to cephalic segments; on hazel; length, 15 mm.; width of head, 1.5 mm.; M-109.  
*modestius* MacGillivray.
- 2(1) Front without a distinct blackish or fuscous spot, but with a light or pale brown spot; vertex with a dorso-mesal fuscous or blackish spot, not nearly occupying the entire space between vertical furrows; body sometimes pinkish; not on hazel. . . . . 3.
- 3(4) Head brown; vertex with blackish spot occupying about one-half the distance between vertical furrows; body pinkish; head with blackish spot caudad of ocellaræ; dorsum of mesothorax to first abdominal segment shaded gray, prothorax whitish; third abdominal segment with the following setal map: 5, 4, 4, 1, 3, 5, 5, 10, 10-12, 6-2; maxillary palpi, 2, (3, 4), 1; in younger specimens body whitish; length, 14 mm.; width of head, 1.2 mm.; on *Salix*; Y-154-1-2. . . . . *palliolatus* MacGillivray.\*
- 4(3) Head pale brown; vertex on dorso-meson with blackish spot occupying two-thirds the distance between vertical furrows; spot also caudad of ocellaræ; body not pinkish but whitish, dorsad of spiracular lines from mesothorax to penultimate

\*This species was described as *Trichiocampus palliolatus* n. sp. by Dr. MacGillivray in the *Entomological News*, vol. XXXII, 1921, page 49, but the characters of the larva place it in the genus *Priophorus*. Upon reexamination of the adult specimens, Dr. MacGillivray agrees with me in the change I here make.



segment distinctly and uniformly olivaceous-gray; third abdominal segment with following setal map: 5-6, 5, 5, 1-2, 3, 6, 6, 10, 15, 8-9; maxillary palpi, 2, 3, (4, 1); in younger specimens black spots on head larger and olivaceous shade on dorsum of body restricted to cephalic segments; length, 16 mm.; width of head, 1.6 mm.; on *Prunus virginicus*; Y-138-3. (This species resembles *P. solitarius* according to Dyar's description but the latter feeds on *Alnus*,.....*Priophorus* sp. 1.

### CLADIUS ROSSI

Larvae rather small; length less than 15 mm.; body slightly flattened, greenish or yellowish green; never with spots or shaded on dorsal half; annulet 1 with a transverse row of several setae, annulet 2 with two warts bearing 5-6 setae, annulet 3 with three warts, dorsal two bearing 6-7 setae, ventral with 10 setae; postsupraspiracular tubercles with 5-6 setae; subspiracular lobe with 14-17 setae, surpedal lobe with 10 setae; setae usually straight, usually of two lengths, longer ones less than half the height of head; setae on annulet 1 among the shortest.

*Cladius pectinicornis* Fourcroy.—Length, 12-14 mm.; head pale brownish or yellowish, microscopically verrucose, with brownish spots; front touched with light brown; body hairy, uniformly greenish or greenish yellow; third abdominal segment with the following setal map: 5-6, 5, 6, 1, 5-6, 6, 7, 10, 14-17, 10; maxillary palpi, (2, 3), 1, 4; on *Rosa*; Y-3, M-244.

### SUBFAMILY NEMATINAE

Larvae (Fig. 18) small to moderately large; body cylindrical, slender, or abdomen increasing in diameter; segmentation and annulation usually distinct; third abdominal segment with 4, 5 or 6 annulets, annulets 1, 2, 3, or 1, 2, 4, or more usually 2 and 4, setiferous; larvapods present on abdominal segments 2-7 and 10, setiferous or sometimes glabrous; ventral glands present on the meson of abdominal segments 1-7; thoracic legs normal in form; body uniformly greenish or darker colored, striped or spotted, tuberculate, setiferous or smooth; antennae with four segments, conical, subconical, limpet-shaped, or flattened; antennal segments sometimes incomplete or in part fused together; tenth abdominal tergum with or without a pair of caudal protuberances; glandubae sometimes distinct, conspicuous, and stalked; spiracles winged or not; larvae free leaf-feeders, gall-makers, and leaf-rollers.

The Nematinae is a large subfamily of several genera and numerous species and is characterized by the coalescence of the cells 2d A and 3d A due to the atrophy of the free part of the 3d anal vein. The absence of the radial cross-vein and the cell 1st 2d A distinguishes the adults of this subfamily from those of the Hoplocampinae and Cladiinae respectively. Rohwer (1912), who would unite the Nematinae, Hoplocampinae, and three genera of the Cladiinae in one subfamily, Nematinae, states that the

subfamily contains two types of larvae and that most of the aberrant larvae belong to his tribe Hemichroini. It may be pointed out that the Nematinae as defined by MacGillivray also contains two types of larvae, which are separable on the presence or absence of the caudal protuberances on the ultimate segment. There are, however, other morphological and biological characters of the larvae which suggest that this subfamily contains a number of genera of wide diversity, and that such genera as *Pteronidea* and *Pontania* might profitably be subdivided into more genera.

#### GENERA OF NEMATINAE

- 1(18) Tenth abdominal tergum without caudal protuberances. . . . . 2.
- 2(11) Antennae conical or subconical, antennal segments 2 and 3 always complete, segment 4 peg-like or conical, at least as long as wide at proximal end; third abdominal segment always with six annulets. . . . . 3.
- 3(4) Annulets 2 and 4 glabrous; larvapods glabrous; glandubae obsolete; thoracic legs with coxae in part always colored brownish. . . . . *Nematus* Panzer.
- 4(3) Annulets 2 and 4 not glabrous; larvapods usually not glabrous; glandubae usually not obsolete; thoracic legs with coxae usually in part not colored. . . . . 5.
- 5(6) Antennae with segment 3 ring-like, its cephalic portion subequal in length to caudal portion, segment 2 complete, its cephalic portion not reduced to a mere line; body increasing in diameter to abdominal segments 5-6; spiracles usually winged; larvapods glabrous or with 2-4 or more setae as viewed from lateral aspect. . . . .  
*Pristiphora* Latreille.
- 6(5) Antennae with segment 3 not ring-like, its cephalic portion not subequal in length to caudal portion; segment 2 usually complete but its cephalic portion reduced to a mere line. . . . . 7.
- 7(8) Body increasing in diameter to abdominal segments 5-6, not uniformly cylindrical; spiracles usually winged; larvapods with 4-6 setae as viewed from lateral aspect. . . . .  
*Diphadnus* Hartig.
- 8(7) Body not increasing in diameter to abdominal segments 5-6 but uniformly cylindrical; spiracles never winged; larvapods with 1-2 setae as viewed from lateral aspect. . . . 9.
- 9(10) Thorax distinctly swollen; head pale brownish green; maxillary palpi with segment 2 as long on its lateral aspect as on its mesal aspect; legs with femur and tibia concolorous with body, whitish; body with dorsum not shaded bluish green. . . . .  
*Pteronidea* Rohwer (in part).
- 10(9) Thorax never distinctly swollen; head not pale brownish green but blackish; maxillary palpi with segment 2 three times as long on its lateral aspect as on its mesal aspect; legs with femur and tibia not concolorous with body but blackish; body with dorsum shaded bluish green. . . . . *Lygaeonematus* Konow.
- 11(2) Antennae not conical or subconical, but flattened; antennal segments 2 and 3 not always complete, segment 4 never peg-like or conical, never as long as wide at proximal end; third abdominal segment not always with six annulets. . . . . 12.
- 12(13) Segments with four annulets, annulets 1, 2, and 3 setiferous; gall-makers. . . . .  
*Pontania* Costa (in part).
- 13(12) Segments with more than four annulets, annulet 1 not setiferous; not gall-makers. . 14.
- 14(15) Segments with five annulets, annulets 2 and 3 setiferous; antennae with all segments fused together; larvapods with two setae as viewed from lateral aspect; body-setae very long. . . . . *Micronematus* Konow.

- 15(14) Segments with five or six annulets, annulets 2 and 4 setiferous; antennae usually not with all segments fused together; larvapoas usually with many more than two setae as viewed from lateral aspect; setae on body not very long; glandubae usually conspicuous and stalked.....16.
- 16(17) Segments with six annulets; larvapoas with 7-10 setae as viewed from lateral aspect; surpedal areas at least in part always marked with gray; latus of abdomen never with numerous brownish spots; tenth abdominal tergum sometimes distinctly pointed and produced caudad and with many conspicuous glandubae near the caudal margin; larvae usually feeding on monocotyledonous plants...*Pachynematus* Konow.
- 17(16) Segments with five annulets; larvapoas with 3-5 setae as viewed from lateral aspect; surpedal areas not marked with gray; latus of abdomen sometimes with numerous brownish spots; tenth abdominal tergum never distinctly pointed and produced caudad; larvae usually feeding upon willow.....*Amauronematus* Konow (in part).
- 18(1) Tenth abdominal tergum with a pair of caudal protuberances.....19.
- 19(20) Gall-makers and leaf-rollers; segments with four annulets; annulets 1, 2, and 3 setiferous; antennae flattened; body setae more than twice as long as spiracles; caudal protuberances normal in form and position or rudimentary or borne on a small caudo-mesal projection, if normal in form and position, the tergum with paired colored markings.....*Pontania* Costa (in part).
- 20(19) Free leaf-feeders; segments usually with five or six annulets, if four, annulets 2 and 4 usually setiferous; antennae conical or flattened.....21.
- 21(22) Antennae conical, segment 2 complete, segment 3 ring-like, its cephalic portion subequal in length to caudal portion; body on latus with eleven conspicuous blackish-brown spots, surpedal and subspiracular areas of abdominal segments 1-9 and venter between larvapoas of abdominal segments 2-8 similarly marked; spiracles not winged; caudal protuberances of ultimate segment small, blunt, not longer than wide at proximal end; segments with five or four annulets, with annulets 2 and 3 or 2 and 4 setiferous.....*Croesus* Leach.
- 22(21) Antennae conical or flattened; if conical, segment 3 not ring-like but reduced in length on cephalic aspect; body not marked as in *Croesus*; spiracles winged or not winged; caudal protuberances of ultimate segments not blunt, minute, but usually much longer than wide at proximal end.....23.
- 23(24) Segments apparently with five annulets; annulets 2 and 3 setiferous; antennae flattened, with segment 3 complete; body-setae subequal in length to spiracles; smaller larvae, length, 13-15 mm.....*Amauronematus* Konow (in part).
- 24(23) Segments with four or six annulets; annulets 2 and 4, rarely 1, 2, and 3, setiferous; antennae conical or flattened, segment 3 complete or incomplete; body-setae often longer than the length of abdominal spiracles; small to moderately large larvae, length, 15-23 mm.....*Pteronidea* Rohwer (in part).

#### DIPHADNUS HARTIG

Larvae small, greenish; length less than 14 mm.; body cylindrical, increasing in size to abdominal segments 5-6, tapering at each end; thorax not swollen; tenth abdominal tergum without a pair of caudal protuberances; third abdominal segment with six annulets, annulets 2 and 4 setiferous; spiracles distinctly and usually equally winged; head marked with black or brown streaks along epicranial stem and dorsad of ocellaræ; somewhat compressed cephalo-caudad; labrum with median emargination broad and deep and with median longitudinal depression; antennae distinctly conical,



with four segments, segment 1 incomplete, segment 2 usually complete tho reduced to a mere line on cephalic part, segment 3 narrowed on cephalic part, segment 4 short, conical, or peg-like; larvapods setiferous, setae 4-6 in number as viewed from lateral aspect; anal larvapods rather large; glandubae sessile; cuticle microscopically spinulate; suranal and subanal lobes with numerous setae; larvae free leaf-feeders.

*Diphadnus appendiculatus* Hartig.—Length, 13 mm.; width of head, 1.35 mm.; body green, venter glossy white; tenth abdominal tergum not marked; head greenish white with blackish brown streak along epicranial stem, except near the occiput, and continuing to the dorsal two-thirds of front, vertex dorsad of each ocellara not quite reaching the epicranial suture; surface of head with minute brownish spots; following parts brown: mandibles at apices, antennae, cervical sclerites, coxae at proximal third, tarsal claws, and spiracles; setae minute, with conspicuous calices, blackish; glandubae smaller at distal end than the calyx of seta; larvapods on cephalic and lateral aspects with 4-6 setae and with a single ventral glanduba; annulation, 1, (6, 2), (3, 5), 4; subspiracular lobe with 5-6 setae and without glandubae; surpedal lobe with about 4 setae and one subsessile glanduba; on gooseberry; Y-158, -159, M-128.

#### PRISTIPHORA LATREILLE

Larvae small, greenish; length less than 15 mm.; body cylindrical usually slightly enlarged at abdominal segments 5-6, tapering at each end; thorax not swollen; tenth abdominal tergum without the paired caudal protuberances; third abdominal tergum with six annulets, annulets 2 and 4 microscopically setiferous, setae sometimes obsolete; annulet 1 always longest and annulet 3 and 4 always shortest; spiracles usually winged, caudal wing usually much smaller than cephalic; head marked usually with a blackish or brownish streak along epicranial stem, surface with minute brown spots; labrum with distinct mesal emargination and longitudinal depression; antennae conical or limpet-shaped, usually with four distinct segments, segment 1 always minute, incomplete on caudal side, segment 2 complete, but usually narrower on cephalic side, segment 3 uniform in length, segment 4 short, conical; larvapods usually glabrous and with a single ventral glanduba, if setiferous, setae microscopic, 2-4 in number as viewed from side; anal larvapods rather conspicuous, glandubae sessile or stalked; cuticle microscopically spinulate, suranal and subanal lobes with numerous setae; tenth abdominal tergum as seen from side notched dorsad of suranal lobe; free leaf-feeders.

#### SPECIES OF PRISTIPHORA

- 1(8) Larvapods setiferous; antennae always conical; head always with a brownish streak dorsad of each ocellara; spiracles always with cephalic wing distinctly larger than



- caudal wing; setae with calices surrounded by minute brownish areas; glandubae always sessile, sometimes microscopic, diameter never more than half the diameter of calices of setae. .... 2.
- 2(3) Glandubae minute but distinct, about one-third as large as calices of setae or microscopic in smaller specimens; annulation, 1, (5, 6), 2, 3, 4; subspiracular area with 3-4 setae; surpedal area with 3-4 setae; larvopods with 2-4 setae as viewed from side; head light brownish-green, marked with fuscous streaks on both sides of entire length of epicranial stem, front with dorsal two-thirds light brown; following parts light brown: labrum, antennae, mandibles, cervical sclerites, tarsal claws, and spiracles; body greenish, caudal segments pinkish or bluish, dorsal vessel dark green with distinct fine white line on each side; Length, 14 mm.; on *Salix*; Y-143-2-2,-155, M-96. *murtfeldtiae* Marlatt.
- 3(2) Glandubae microscopic, difficult to detect. .... 4.
- 4(5) Second annulet of abdominal segments always longer than either fifth or sixth annulet; larvopods with about two setae as viewed from side; subspiracular areas with 4-5 setae, surpedal areas with 4 setae; annulation, 1, (5, 6), 2, 4, 3; on birch; M-24. .... *Pristiphora* sp. 1.
- 5(4) Second annulet of abdominal segments always shorter than either annulet 5 or 6; larvopods with 1-2 or 2-4 setae as viewed from side; subspiracular areas with four setae; on alder or willow. .... 6.
- 6(7) Larvopods with 1-2 setae as viewed from side; annulation 1, 2, (4, 5, 6), 3; surpedal areas with 3-5 setae; body green, cylindrical; head pale brownish-green, marked with brown streak along entire length of epicranial stem and dorsal two-thirds of front and vertex, narrowly dorsad of each ocellara; following parts brown: antennae, labrum, mandibles, maxillary palpi, cervical sclerites, tarsal claws, and spiracles; antennae conical, segment 4 short, conical; spiracle with cephalic wing distinctly longer than caudal; setae without brown areas surrounding calices; glandubae minute, sessile, microscopic; M-74. .... *Pristiphora* sp. 2.
- 7(6) Larvopods with 2-4 setae as viewed from side; surpedal areas with 3-5 setae; annulation, 1, 2, 6, 5, 4, 3; on woolly willow; M-90. .... *Pristiphora* sp. 3.
- 8(1) Larvopods glabrous; antennae conical or limpet-shaped; head with or without a dark streak dorsad of each ocellara; spiracles winged or not winged, if winged, wings subequal in size, or cephalic wings larger than caudal; setae usually with calices surrounded by minute but distinct brownish areas; glandubae sessile or stalked, sometimes microscopic. .... 9.
- 9(10) Head distinctly and uniformly brownish; spiracles indistinctly winged; all setae ventrad of subdorsal lines with calices surrounded by minute brownish areas; antennae conical; glandubae subequal to calices in diameter; annulation, 1, 5, 6, 2, 3, 4; on birch; M-132. .... *Pristiphora* sp. 4.
- 10(9) Head never distinctly and uniformly brownish. .... 11.
- 11(12) Body on dorso-meson from prothorax to fifth abdominal segment with a distinct blackish line; spiracles winged, cephalic wings usually larger than caudal; all setae ventrad of subdorsal lines with calices surrounded by minute brownish areas; antennae conical; glandubae minute, about half as large as calices in diameter; head with distinct line along epicranial stem; vertex without a dark streak dorsad of each ocellara; annulation, 1, 2, (5, 3, 4, 6) or 1, 2, (3, 4, 5, 6); on *Prunus*; M-128. .... *Pristiphora* sp. 5.
- 12(11) Body on dorso-meson from prothorax to fifth abdominal segment without a distinct blackish line. .... 13.
- 13(14) Head entirely pale or light brown; vertex without dark streak along epicranial stem, antennae distinctly conical; spiracles winged, wings subequal in size; setae never with

- calices surrounded by distinct brownish areas; glandubae probably obsolete, microscopic; annulation, 1, 5, 6, 2, 3, 4; on oak; M-20.....*Pristiphora* sp. 6.
- 14(13) Head never entirely pale or light brown; vertex always with a dark streak along epicranial stem, sometimes indistinct but never entirely wanting.....15.
- 15(22) Spiracles winged; setae ventrad of spiracular lines with calices surrounded by distinct minute brownish areas; antennae always conical; vertex with or without a dark streak dorsad of each ocellara.....16.
- 16(19) Spiracles with cephalic wings always larger than caudal; glandubae always sessile; glandos microscopic, difficult to detect; setae on latius dorsad of spiracular lines with calices surrounded or not surrounded by distinct brownish areas.....17.
- 17(18) All setae on latius dorsad of spiracular lines with calices surrounded by brownish areas; vertex dorsad of each ocellara with a brownish streak; annulation, 1, (5, 6), 2, 4, 3; body green; head marked as in *P. bivittata*; length of body, 12-13 mm.; on *Salix*; M-72.....*syphophanta* Walsh.
- 18(17) All setae on latius dorsad of spiracular lines with calices not surrounded by brownish areas; vertex dorsad of each ocellara without a brownish streak, uniformly pale; annulation, 1, (2, 5, 6), 4, 3; body enlarged on abdominal segments 5-6, greenish, with dorsal vessel dark green with white line on each side; head greenish with brownish streaks along entire length of epicranial stem, expanding on the dorsal half of front; following parts brown: labrum, mandibles, antennae, cervical sclerites, tarsal claws, and spiracles; antennae conical, segment 4 elongate, conical; on *Spiraea latifolia* and *S. tomentosa*; M-4.....*Pristiphora* sp. 7.
- 19(16) Spiracles with wings subequal in size; glandubae stalked; glandos subequal in diameter to calices; setae on latius dorsad of spiracular lines never with calices surrounded by distinct brownish areas.....20.
- 20(21) Vertex with a distinct dark streak dorsad of each ocellara; annulation, 1, 2, (5, 6), 4, 3; length, 16-17 mm.; body cylindrical, increasing in size to abdominal segments 5-6, green, dorsal vessel dark green with fine white line on each side of it; head green, slightly brownish, with fuscous streaks; following parts light brown: dorsal two-thirds of front, labrum, maxillary palpi and galea, labial palpi, and cervical sclerites; following parts brown: antennae, mandibles, spiracles, glandubae, and setae; antennae conical, distinctly with four setae, segment 4 conical; spiracles with wings; ventral glands subequal in size to larvopods; glandos in diameter subequal to or larger than calices of setae; setae on dorsum very minute; on *Spirea*; Y, M-14, 88.....*bivittata* Norton.
- 21(20) Vertex without a distinct dark streak dorsad of each ocellara; annulation, 1, 2, 6, 5, 3, 4; on *Potentilla*; M-10.....*Pristiphora* sp. 8.
- 22(15) Spiracles not winged; setae ventrad of spiracular lines never with calices surrounded by distinct minute brownish areas; antennae limpet-shaped, segments indistinguishably fused; vertex always with a brown streak dorsad of each ocellara; glandubae sessile; glandos microscopic, difficult to detect; annulation, 1, (2, 5, 6), (3, 4); length 12-13 mm.; body green, with broad dark green dorsal vessel bordered on each side by a fine white line; head greenish brown; setae stiff, comparatively long, without brown areas surrounding calices; on *Geum canadensis*; Y-212..*Pristiphora* sp. 9.

#### MICRONEMATUS KONOW

Larvae small; length less than 15 mm.; body subcylindrical, tapering at both ends; mesothorax distinctly and metathorax slightly swollen; lateral lobes prominent and swollen; segmentation distinct; annulation indistinct; third abdominal segment with five annulets, annulets 2 and

3 setiferous; thoracic legs spreading laterad, normal in form; larvapods setiferous, normal in form, except the anal pair, which is reduced in size, only one-half as large as the other pairs; tenth abdominal tergum without the paired caudal protuberances; head circular, smaller than thorax in width and height, front flattened; antennae apparently with four segments, flattened, all segments fused together; ventral glands very large; setae sparse, very long; spiracles not winged; suranal and subanal lobes multisetiferous; glandubae sessile; free leaf-feeders.

Konow in 1905 listed three species of *Micronematus*: *abbreviatus*, *californicus*, and *monogyniae*. The second species properly belongs to *Diphadnus*. Of the two remaining species, *M. abbreviatus* was recognized in the larval stages a long time ago by Snellen von Vollenhoven (1868). This genus is European and is represented in North America by a single species, *Micronematus gregarius* Marlatt. That this species does not belong to *Pachynematus* can be readily seen from the structure and biological characters of the larvae as was suggested by Dyar (1897) in his original description of the immature stages. Three facts distinguish this species from all other known species of *Pachynematus*: (1) the larva has five annulets instead of six; (2) the anal larvapods are very much reduced in size; and (3) the larva feeds on willow instead of grasses. On the other hand *M. gregarius* has certain characters in common with *M. abbreviatus* as recorded by Vollenhoven. Since this species can not be referred to *Pachynematus* or to any other known American genus, and since it has characters which are peculiar to *Micronematus*, and since the adult characters, according to Ashmead (1898), would place it in this genus, this species is here considered as belonging to *Micronematus*. If future study should prove this position untenable, a new genus should be erected.

*Micronematus gregarius* Marlatt.—Length, 12 mm.; body shiny, yellowish white; alimentary canal showing thru as green tube; head pale testaceous with a broad blackish band across the front between ocellaræ and a narrow band dorsad of each ocellaræ to and along vertical furrow; mouth-parts, cervical sclerites, and legs except coriæ brownish; abdominal segments 1-8 with postspiracular and subspiracular areas swollen, mound-like, and tinted fuscous; abdominal segments 2-7 with colored postspiracular areas larger than subspiracular areas; those on segments 1 and 8 much smaller; thoracic segments with two colored patches on *latus*, one larger and more ventral than the other; larvapods with about two setae on the cephalo-lateral aspect; ventral glands nearly three times as large as larvapods; setae slender, at least twice as long as spiracles; spiracles not winged; subspiracular area with two setae and single glanduba, surpedal area with 3-4 setae and single glanduba; larvae gregarious; on *Salix*; Y.



## LYGAEONEMATUS KONOW

Larvae comparatively speaking moderately large, length 18–20 mm.; body cylindrical, tapering uniformly and slightly caudad; thorax not swollen; abdomen never swollen; dorsum grayish green and venter pale, head shiny black, only slightly narrower than thorax; antennae conical, with four distinct segments, segment 1 minute, incomplete, and with single sensory pit, segments 2 and 3 narrower on cephalic part than on caudal part, segment 4 conical; labrum with mesal emargination shallow and broad; maxillae with galea larger than labial palpi; maxillary palpi with segment 2 three times as long on lateral margin as on mesal; third abdominal segment with six annulets, annulet 1 largest, annulets 2 and 4 setiferous; larvapods well developed, setiferous, with 1-2 setae and single ventral glanduba; glandubae sessile; glandos smaller than calyx of a seta; ventral glands subequal to or larger than larvapods in size; spiracles not winged; tenth abdominal tergum as seen in profile not notched dorsad of suranal lobe and without caudal paired protuberances; setae usually arising from minute fleshy mound-like protuberances; cuticle microscopically spinulate; free leaf-feeders.

*Lygaeonematus erichsoni* Hartig.—Length, 18-20 mm.; body somewhat shiny, greenish gray dorsad of spiracular lines, ventrad of them opaque bluish-white, head black; following parts fuscous to blackish: mouth-parts, cervical sclerites, femur, tibia, and claws; following parts grayish: surpedal areas, coxa, and trochanter in part, swellings between legs, and abdominal surpedal areas faintly; annulation, 1, 2, 6, (3, 5, 4); glandos half as large in diameter as calices of adjacent setae; surpedal areas on abdomen with 8-10 setae and two glandubae; subspiracular area with 6-7 setae, usually without glandubae; cuticle with distinct microscopic brownish spinulae; on larch; Y-162, M-105, -165.

## PACHYNEMATUS KONOW

Larvae comparatively speaking moderately large; length, 15–23 mm.; body cylindrical, tapering uniformly and distinctly caudad; thorax rarely and abdomen never swollen; third abdominal segment with six annulets, annulets 2 and 4 setiferous, annulet 1 longest, annulet 4 usually shortest; tenth abdominal tergum without a pair of caudal protuberance, and without a notch dorsad of suranal lobe as seen in profile; the tergum sometimes produced distinctly caudad and pointed; suranal and subanal lobes with numerous setae; head brownish or greenish, sometimes with fuscous streak along epicranial stem, semiglobose, subequal in width to thorax or only slightly narrower; labrum with median longitudinal depression, cephalic emargination shallow; maxillae with galea always larger than labial palpi, sometimes more than twice as large; antennae with four segments, flattened, never distinctly conical, segment 1 usually minute, in-



complete, segments 2 and 3 with cephalic parts distinctly reduced to mere lines, sometimes all four segments fused; larvapods always setiferous, with 8-11 setae on cephalic and lateral aspects and a single ventral glanduba; glandubae conspicuous, cylindro-conical, at least twice as long as wide at proximal end; spiracles usually not winged, if winged, rather indistinctly; setae stiff, brown, arising from fleshy mound-like minute tubercles; in younger specimens third abdominal segment with five annulets, annulets 1, 2, and 3 with stiff brown setae; glandubae obsolete; cuticle microscopically spinulate; larvae usually feed upon grasses.

This generic description is based upon two identified and several unidentified species. The known species can be separated as follows:

#### SPECIES OF PACHYNEMATUS

Head with narrow fuscous or blackish streak along epicranial stem and vertical furrows; tenth abdominal tergum with a broad fuscous streak on the meson and the caudal margin produced distinctly caudad and bluntly pointed, with many conspicuous glandubae; antennae with four fused segments; annulation, (2, 1), 6, (3, 4, 5); larvapods with 7-9 setae on cephalic and 1 seta on lateral aspect; subspiracular lobe with 5-6 setae and 1-2 glandubae; surpedal lobe with 5-7 setae and 1-3 glandubae; body on dorso-lateral lines with narrow, interrupted longitudinal fuscous, bands; head as wide as thorax; length, 20 mm. width of head, 2 mm.; on *Carex*; Y-150.....*subalbatus* Norton.

Head with narrow fuscous or blackish streak along epicranial stem and vertical furrows; tenth abdominal tergum without a broad fuscous streak on the meson, the caudal margin only slightly produced caudad, rounded, with many glandubae; antennae with four segments not fused; annulation, (1, 2), 6, (3, 4, 5); larvapods with about ten setae on cephalic and one seta on lateral aspect; subspiracular lobe with about six setae and a single glanduba; surpedal lobe with six setae and three glandubae; head as wide as thorax; length, 16 mm.; width of head, 1.6 mm.; on *Carex*; Y-177.....*reperitus* MacGillivray.

#### NEMATUS PANZER

Larvae comparatively small, length about 10 mm.; body cylindrical, uniform in diameter thruout the entire length excepting the caudal end, where it is tapering, dull green, apparently glabrous; annulation indistinct; third abdominal segment with six annulets, annulets glabrous, formula: 1, 5, 2, 6, 3, 4; thoracic legs normal in form; coxa usually fuscous on proximal half; larvapods small, diminishing in size gradually on the caudal segments, not setiferous; ventral glands subequal in size to larvapods; tenth abdominal tergum without a pair of caudal protuberances, with a notch dorsad of suranal lobe as seen in profile, caudal margin truncate or slightly emarginate on the meson, not produced; suranal lobe with several minute setae on ventral aspect; subanal lobe with moderately numerous minute setae; abdomen with lateral lobes inconspicuously swollen; head circular in outline, rounded in profile on dorsal half, front flattened; ventral half of head with several longer and larger setae; dorsal half nearly glabrous or with microscopic setae; vertex usually with a fuscous

streak caudad and dorsad of each ocellara; antennae four-segmented, subconical or sublimpet-shaped, sometimes in part fused; segment 1 minute, segments 2 and 3 reduced to mere line on cephalic aspect, segment 4 minute, subconical; mouth-parts and cervical sclerites fuscous to blackish; maxillary palpi with two distal segments distinctly smaller than segment 2, which is sometimes longer than all the other segments taken together; galea larger than labial palpus; sericos distinct, circular; subspiracular and surpedal lobes with a few microscopic setae; glandubae probably microscopic, usually obsolete; spiracles usually winged; cuticle microscopically spinulate; free leaf-feeders.

#### SPECIES OF NEMATUS

- 1(4) Vertex with a fuscous streak caudad and dorsad of each ocellara; maxillary palpi with segment 2 shorter than all the other segments taken together. . . . . 2.
- 2(3) Vertex with fuscous streaks extending dorsad of vertical furrows; antennae with all segments fused and almost completely filling antafossae; spiracles distinctly winged; tenth abdominal tergum with caudal margin shallowly emarginate on the meson; head with dorsal half entirely glabrous; length, 11 mm.; on oak; M-21. . . *chloreus* Norton.
- 3(2) Vertex with fuscous streaks not extending dorsad of vertical furrows; antennae with all segments distinct, but not nearly completely filling antafossae; spiracles not distinctly winged; tenth abdominal tergum with caudal margin not emarginate on the meson; head with dorsal half sparsely setiferous; length, 9 mm.; Y-133. *Nematus* sp. 1.
- 4(1) Vertex without a fuscous streak caudad and dorsad of each ocellara; maxillary palpi with segment 2 slightly longer than all the other segments taken together; antennae with four distinct segments; spiracles winged; length, 10.5 mm.; on oak; M-2. *Nematus* sp. 2

#### CROESUS LEACH

Larvae moderately large, length about 25 mm., body cylindrical tapering caudad on abdominal segments 7-10 and also at cephalic end of prothorax; segmentation distinct; annulation indistinct; third abdominal segment with four or five annulets, annulets 2 and 3 setiferous; tenth abdominal tergum with a pair of low, conical, bluntly rounded caudal protuberances, usually as wide as or wider than high; head flattened on front, rounded, shiny black; antennae distinctly conical with four segments: segment 1 incomplete, three times as long as wide, segments 2 and 3 usually complete and not reduced to mere lines on the cephalic aspect, segment 4 peg-like, bluntly pointed, longer than wide at proximal end; maxillary palpi with segment 1, 3, and 4 subequal in length, segment 2 twice as long as segment 1; larvapods setiferous; spiracles not winged, indistinctly colored; glandubae subsessile or with a short stalk, very wide in diameter more than three times the diameter of shaft of setae; maxacoria developed into a distinct triangular swelling dorso-caudad of cardo, and covered with dark spinulae.

*Croesus latitarsus* Norton.—Length, 25 mm.; annulation, 3, 2, 1, 4 or 2, 1, 5, 3, 4; larvapods with 4-5 setae and a single glanduba as viewed from side, no markings; tenth abdominal tergum with dark-colored area

contiguous to concolorous suranal protuberances; suranal and subanal lobes with numerous setae, which increase in length with the distance from the anus; body yellowish green or brownish, with colored patches on subspiracular and surpedal areas and on subdorsal line from mesothorax to ninth abdominal segment; abdominal segments 2-8 on ventro-meson each with a large colored patch; in younger stages body fuscous with few distinctly delimited colored patches or none; M-1,-26,-50,-51,-48.

#### AMAURONEMATUS KONOW

Larvae small to moderately large; length 15-20 mm.; body cylindrical, often tapering distinctly caudad; latus with subspiracular and surpedal areas colored or with numerous, minute colored spots; head blackish, brownish, or greenish; third abdominal segment with five annulets, annulets 2 and 3 or 2 and 4 setiferous; tenth abdominal tergum with or without caudal paired protuberances; body setae much longer or shorter than the length of spiracles; larvapods with 2-3 or 3-5 setae as viewed from side; spiracles not winged; larvae free leaf-feeders.

The larval stages of five species of *Amauronematus* have been described by Dyar. Of these, larvae of *luteotergum*, *dyari*, *oregonensis*, and *similis* have not been available for study, but according to Dyar's descriptions, the last three apparently lack the caudal paired protuberances. I have a large number of larvae collected on willow by Dr. MacGillivray which also lack the paired caudal protuberances and probably belong to this genus. The species may be separated as follows:

#### SPECIES OF AMAURONEMATUS

- 1(4) Tenth abdominal segment with paired caudal protuberances.....2.
- 2(3) Abdomen on ventro-meson with a row of blackish spots; caudal paired protuberances and head blackish; gregarious; on alder.....*luteotergum* Norton.
- 3(2) Abdomen on ventro-meson without a row of blackish spots; paired caudal protuberances and head not blackish but pale; solitary; on Azalea.....*azaleae* Marlatt.
- 4(1) Tenth abdominal segment without paired caudal protuberances.....5.
- 5(6) Mature and also younger larvae with antennae flattened and their segments fused in part, with no discernible or with very small antacoria; younger larvae (14 mm. or less) with annulets 1, 2 and 4 setiferous; annulets 2 and 4 with transverse row of warty protuberances each bearing 2 or 3 stiff stout setae; older larvae (14 mm. or more) without numerous brownish spots on dorsum and latus and without brownish interrupted and diffuse dorso-mesal and dorso-lateral lines; on sweet fern; M-85.  
*Amauronematus* sp. 1.
- 6(5) Mature larvae with antennae whose segments are all distinctly separated by distinct antacoria; young larvae with antennae like those of preceding species; younger larvae (14 mm. or less) with annulets 1, 2, and 4 setiferous; annulets 2 and 4 without transverse row of warty protuberances the setae being minute and arranged singly; older larvae (14 mm. or more) with numerous brownish spots on dorsum and latus with brownish, interrupted, and diffuse dorso-mesal and dorso-lateral lines; on willow; M-10.....*virendus* MacGillivray.



Another species, resembling the preceding very closely and, difficult to distinguish except by the colored spots which are more or less darker and slightly more numerous than in *virendus*; M-112.....*vescus* MacGillivray.

#### PTERONIDEA ROHWER

Larvae small to moderately large; length 15-25 mm.; greenish, often spotted or banded transversely or longitudinally; body cylindrical, slender, uniformly tapering caudad, thorax rarely conspicuously swollen; head and trunk setiferous, often tuberculate; head blackish, brownish, or greenish; antennae with four segments, sometimes with segments in part fused, conical, subconical, or flattened; third abdominal segment with 4-6 annulets, more commonly 5-6, annulets 2 and 4, rarely 1, 2, and 3 setiferous; tenth abdominal tergum with or without a pair of small but distinct suranal caudal protuberances, if without, body swollen on thorax, protuberances pointed, bluntly rounded, truncate, or swollen at distal end; larvapods setiferous, setae few in number; spiracles winged or unwinged; glandubae subsessile or obsolete; leaf-feeders, sometimes gregarious.

The genus *Pteronidea* is rich in number of species. The author has examined a large number of specimens representing at least thirty species and including much bred material, and has prepared the following synoptic key for differentiating species. It may be stated here that *Pteronidea*, together with a few allied genera, is readily separated from all other Tenthredinidae by the presence of a pair of suranal caudal protuberances on the lateral portion of the caudal margin of the ultimate tergum. *Pteronidea thoracica* Harrington is unique in lacking the caudal paired protuberances, but is easily distinguished by its characteristic, somewhat elongate, tadpole-like body, and also by its white head and body and its spreading legs. The color and coloration and the presence of setiferous tubercles and their arrangement are useful characters in separating species.

#### SPECIES OF PTERONIDEA

- |       |  |  |
|-------|--|--|
| 1(2)  | Tenth abdominal tergum without suranal processes; thorax conspicuously swollen; thoracic legs spreading out flat laterad; body entirely greenish white; on <i>Prunus virginiana</i> ; Y-141..... | <i>thoracica</i> Harrington.           |
| 2(1)  | Tenth abdominal tergum with suranal processes; thorax not conspicuously swollen.   | 3.                                     |
| 3(50) | Head black or brown; body usually with numerous colored patches.....   | 4.                                     |
| 4(5)  | Body entirely blackish with distinct yellowish spots on <i>latus</i> ; on <i>Salix</i> , <i>Populus balsamifera</i> , etc.; Y-8.45, M-104, M-182, Y-5-2.....                                     | <i>ventralis</i> Say.                  |
| 5(4)  | Body not entirely blackish, without distinct yellowish spots on <i>latus</i> .....   | 6.                                     |
| 6(7)  | Body entirely green; head light brown; suranal processes short, mere swellings; on <i>Ribes</i> sp.; Y-1.....  | <i>ribesi</i> Scopoli (ultimate stage) |
| 7(6)  | Body not entirely green; suranal processes usually distinctly pointed, more than mere swellings.....   | 8.                                     |
| 8(9)  | Body yellowish with 11 transverse black markings extending between subdorsal lines across the venter. Young collection 55.....   | <i>Pteronidia</i> , sp. 1.             |
| 9(8)  | Body not yellowish, without 11 transverse blackish markings.....   | 10.                                    |



- 10(17) Body without numerous small tuberculate areas, usually without fine longitudinal series of sub-adjacent patches; thorax, at least, always suffused on dorsum with darker shade. .... 11.
- 11(12) Body shiny metallic fuscous; dorsum of all segments grayish brown; tenth abdominal tergum uniformly black; Y-132-2-1 (on *Carpinus caroliniana*), Y-132m-1-2 (on *Morus alba*), Y-193 (on *Alnus rugosa*), ..... *erythrogastra* Norton.
- 12(11) Body not shiny metallic fuscous; dorsum of none of segments grayish-brown; tenth abdominal tergum not uniformly black. .... 13.
- 13(14) Abdomen on dorso-meson with a fine longitudinal line; tenth abdominal tergum fuscous on dorso-meson; suranal processes distinctly fuscous; on *Alnus*; M-114. .... *Pteronidea* sp. 2.
- 14(13) Abdomen on dorso-meson without a fine longitudinal line; tenth abdominal tergum not fuscous on dorso-meson; suranal processes not distinctly fuscous. .... 15.
- 15(16) Tenth abdominal tergum with a fuscous triangular mark on each side of meson; head more or less uniformly brown; on *Salix rostrata*; Y-169, C-427-45. .... *Pteronidea* sp. 3.
- 16(15) Tenth abdominal tergum without a fuscous triangular mark on each side of meson; head not uniformly brown but epicranial stem, vertex dorsad of ocellaræ, front in the center, and labrum distinctly darker; on hazel (?); M-153. .... *Pteronidea* sp. 4.
- 17(10) Body with numerous small blackish tuberculate areas; sometimes with fine interrupted longitudinal lines composed of irregular subadjacent colored areas; thorax on dorsum never suffused with darker shade. .... 18.
- 18(27) Body on dorso-meson with a fine more or less continuous black line independent of greenish or pale dorsal vessel, line occasionally faint but never entirely obsolete; latus usually with fine more or less continuous longitudinal lines. .... 19.
- 19(20) Abdomen on ventro-meson with fuscous spots; larvapods on cephalic surpedal areas never with fuscous spots; on *Alnus*; M-232. .... *Pteronidea* sp. 5.
- 20(19) Abdomen on ventro-meson never with fuscous spots; larvapods on cephalic surpedal areas often with fuscous spots. .... 21.
- 21(24) Antennæ with antacoriæ distinct, not limited to periphery of antafossæ; antennal segment 1 very minute, never more than twice as long as wide; segment 2 usually incomplete, if complete, ventral portion never more than a mere faint line; segment 3 usually complete, cephalic portion reduced to a line. .... 22.
- 22(23) Larvapods on cephalic aspect with minute irregular blackish or brownish spots near setæ; on *Salix*; Y-8.48(?) -1. .... *Pteronidea* sp. 6.
- 23(22) Larvapods on cephalic aspect without minute irregular black spots near setæ; on *Salix* spp.; Y-6-1, -6-6, -44-1-1, M-156 (in part), C-140, C-649. .... *odoratus* Dyar.
- 24(21) Antennæ with antacoriæ indistinct, limited to periphery of antafossæ; antennal segment 1 complete, or if incomplete, never less than twice as long as wide; segments 2 and 3 always complete, their cephalic and dorsal portions never reduced to mere lines; segment 4 cylindro-conical; all four segments often fused together in part and filling antafossæ almost completely; larvapods on cephalic aspect with irregular black spots near setæ, spots sometimes very minute but never wanting from all larvapods. .... 25.
- 25(26) Antennæ with all 4 segments fused together in part and filling antafossæ almost completely; on *Salix* spp.; Y-95-1-1, Y-8.45(?) -1. .... *cornelli* Marlatt.
- 26(25) Antennæ without all 4 segments fused together in part; segment 1 always distinctly separated from the other segments; antacoriæ always distinct; on *Populus*; M-156 (in part). .... *Pteronidea* sp. 7.
- 27(18) Body on dorso-meson never with a fine more or less continuous black line independent of greenish or pale dorsal vessel; latus usually without fine more or less continuous longitudinal lines. .... 28.

- 28(29) Latus with distinct more or less continuous longitudinal lines; venter on meson without black spots; C-713.....*Pteronidea* sp. 8.
- 29(28) Latus without distinct more or less continuous longitudinal lines; venter on meson usually with black spots.....30.
- 30(31) Larvapods always with black spots on cephalic aspect; dorsum with setiferous black tubercles more or less uniform in size; abdomen on ventro-meson without black spots; on *Ribes* sp.; Y-1; M-135.....*ribesi* Scopoli.
- 31(30) Larvapods never with black spots on cephalic aspect; dorsum with setiferous black tubercles never uniform in size; abdomen usually with black spots on ventro-meson.32.
- 32(33) Larvapods on abdominal segments 4-7 usually with minute black spots on mesal aspect, those on sixth abdominal segment never wanting; abdomen on ventro-meson without black spots; on *Salix*; Y-95-1; M-155 (in part); M-140.....*Pteronidea* sp. 9.
- 33(32) Larvapods on abdominal segments 4-7 without minute black spots on mesal aspect; abdomen on ventro-meson with black spots.....34.
- 34(47) Abdominal segments 7-9 on ventro-meson with black spots.....35.
- 35(40) Ninth abdominal tergum with colored patches on first three annulets, 4, 6, and 4 patches respectively.....36.
- 36(39) Dorsum not shaded grayish-brown.....37.
- 37(38) On *Populus*; G-14; M-158.....*effeta* MacGillivray.
- 38(37) On *hazel*; M-110.....*effusa* MacGillivray.
- 39(36) Dorsum shaded grayish-brown; on *Salix*; Y-8.45(?) -2-1.....*Pteronidea* sp. 10.
- 40(35) Ninth abdominal tergum with colored patches on first three annulets.....41.
- 41(44) Colored patches on first three annulets 2, 6 and 4 in number respectively.....42.
- 42(43) Body small, less than 13 mm. in length; Young-49.....*Pteronidea* sp. 11.
- 43(42) Body large, more than 15 mm. in length; on *Populus balsamifera*; M-182; G-pop.  
*Pteronidea* sp. 12.
- 44(41) Colored patches on first three annulets 2, 4, and 4 in number respectively.....45.
- 45(46) On *birch*; M-139.....*emerita* MacGillivray.
- 46(45) On *Populus*; Y-45.....*lombardae* Marlatt.
- 47(34) Abdominal segments 2-8 on ventro-meson with black spots.....48.
- 48(49) Large larvae, 20-23 mm. in length; dorsum without dark shade; head much smaller than thorax in width and height; on *Salix*; Y-8.45(?) s-5-2. *fulvicrus* Provancher.
- 49(48) Moderately large larvae, less than 20 mm. in length; dorsum always with dark shade; head comparatively large, only slightly smaller than thorax in width and height; on *Salix*; M-119.....*evanida* MacGillivray.
- 50(3) Head not black or brown, usually greenish with few linear markings; body usually without numerous colored patches.....51.
- 51(54) Body with a pair of distinct fine latero-dorsal lines; larvapods with 1-2 setae as viewed from side.....52.
- 52(53) Head with a black line extending the entire length of epicranial stem to the occiput; on *Salix*; M-12.....*erudita* MacGillivray.
- 53(52) Head without black line extending the entire length of epicranial stem to the occiput; on *Salix*; M-190.....*Pteronidea* sp. 13.
- 54(51) Body without a pair of distinct fine dorso-lateral lines; larvapods usually with 3-5 setae as viewed from side.....55.
- 55(58) Head entirely green.....58.
- 56(57) Suranal process sharply pointed; on *Rhododendron canadense*; M-46.....*Pteronidea* sp. 14.
- 57(56) Suranal processes bluntly rounded; on *Salix*; M-133.....*Pteronidea* sp. 15.

- 58(55) Head not entirely green, usually with a blackish or brownish line along epicranial stem and one dorsad of each ocellar.....59.
- 59(64) Suranal process sharply pointed.....60.
- 60(61) Body tapering caudad uniformly and slightly; uniformly green; on *Salix cordata*; Y-153-1-1,-153-?.....*mendica* Walsh.
- 61(60) Body not tapering caudad uniformly and slightly; abdomen swollen on segments 5-7; body not uniformly green.....62.
- 62(63) Latus of each segment with a large fuscous patch; tenth abdominal tergum with caudal margin between suranal processes straight; on *Alnus*; M-71.....*equina* MacGillivray.
- 63(62) Latus of each segment without a large fuscous patch; tenth abdominal tergum with caudal margin between suranal processes convex; on birch; M-61. *Pteronidea* sp. 16.
- 64(59) Suranal processes never sharply pointed but enlarged at distal ends.....65.
- 65(66) Antennae with segment 3 complete, altho reduced to a mere line on cephalic aspect; on birch; M-60.....*Pteronidea* sp. 17.
- 66(65) Antennae with segment 3 incomplete; Y-120 (on *Gleditsia triacanthos*); Y-143-1 on *Salix cordata*.....*trilineata* Norton.

### PONTANIA COSTA

Larvae comparatively small, whitish or greenish, usually 10-15 mm. in length; gall-makers or leaf-edge-rollers; body cylindrical, thorax usually not swollen; tenth abdominal tergum usually with a pair of suranal protuberances; when the paired caudal protuberances are normal in position, i. e., near the lateral ends of caudal margin of the segment, the tergum usually with paired blackish or brownish markings; caudal protuberances sometimes very minute and borne on the caudal margin of the produced median projection; spiracles winged or not winged; third abdominal segment with four annulets, annulets 1-3 setiferous; head usually dark brown or blackish in younger specimens and yellowish or pale brown in older specimens; labrum with mesal emargination shallow or obsolete; maxillary palpi with segment 2 longest, usually nearly equal in length to segments 3 and 4 taken together; antennae with four segments, segments fused or separate, segments 1 and 2 usually incomplete and separate, segment 3 sometimes complete, often fused with segment 4; larvapods setiferous, with four or more setae.

Most Nematinae with gall-making or leaf-folding larvae belong to this genus. The different types of galls are supposed to be specific and are considered of systematic value. Many species are indistinguishable in the immature stages except by the morphology of the galls they produce.

### SPECIES OF PONTANIA

#### 1. Gall-Makers

- 1(18) Tenth abdominal tergum with or without the paired caudal protuberances, if present, small, blunt, usually not longer than wide at proximal end, sometimes borne on caudal projection of suranal lobe; tergum without paired blackish or brownish markings; ninth abdominal tergum with distinct paired markings or transverse rows of minute spots.....2.



- 2(3) Tenth abdominal tergum without paired caudal protuberances; tibia distinctly longer than femur; head brownish or yellowish with space between ocellaræ across the front paler; Y-8-4-1, -8-4-3, -8-6-1, C-y67, M-212; on *Salix* . . . . . *pomum* Walsh.
- 3(2) Tenth abdominal tergum with paired caudal protuberances; tibia not distinctly longer than femur . . . . . 4.
- 4(5) Suranal lobe not produced caudad, as a small mesal projection, but with a pair of caudal protuberances, small but normal in position, near the lateral ends of the caudal margin; head blackish or blackish brown, space along epicranial suture paler; spiracles usually not winged; dorsum of segments not transversely marked with gray; on *Salix*; Y-7-1, -7-4-1, -8-8, C-cu 201, M-92 . . . . . *hyalina* Norton.
- 5(4) Suranal lobe produced caudad, forming a small mesal projection which bears rudimentary paired protuberances; head light brown with front and vertex dorsad of each ocellaræ darker; spiracles usually winged; dorsum of segments transversely marked with gray; antennæ with segments 3 and 4 fused; labrum with mesal emargination obsolete . . . . . 6.
- 6(7) Gall not transected by the leaf, but attached to one surface, point of attachment showing as discolored scar; greater part of gall free from the leaf; two or more galls sometimes adjacent; woolly small-leaved willows; M-148 . . . . . *Pontania* sp. 1.
- 7(6) Gall transecting the leaf; usually only one gall on a leaf . . . . . 8.
- 8(9) Gall involving the midrib; surface of gall irregularly constricted; sometimes 2 or more galls adjacent; M-226 . . . . . *devincta* MacGillivray.
- 9(8) Gall not involving the midrib tho extending to it . . . . . 10.
- 10(15) Long axis of gall parallel to midrib; leaf transecting the gall into two subequal parts . . . . . 11.
- 11(12) Gall kidney-shaped, strongly convex, about 14 mm. in length; M-213. *Pontania* sp. 2.
- 12(11) Gall not kidney-shaped . . . . . 13.
- 13(14) Gall bean-shaped, slightly convex; 12-14 mm. in length; Y-191-1-1 . . . . .  
*demissa* MacGillivray.
- 14(13) Gall bean-shaped, strongly convex; 14-15 mm. in length; M-262. *Pontania* sp. 3.
- 15(10) Long axis of gall transverse to midrib . . . . . 16.
- 16(17) Gall transected by leaf into two subequal semiglobose parts, surface not constricted by a furrow; M-211, -216 . . . . . *Pontania* sp. 4.
- 17(16) Gall transected by leaf into two unequal parts; surface constricted by a furrow; M-93 . . . . . *Pontania* sp. 5.

## 2. Leaf-folders

- 18(1) Tenth abdominal tergum always with the paired caudal protuberances which are sharply pointed, normal in position, and longer than wide at proximal end; tergum usually with paired blackish or brownish markings; ninth abdominal tergum with or without distinct paired markings or transverse rows of minute spots . . . . . 19.
- 19(20) Tenth abdominal tergum without distinct paired blackish or brownish markings; head entirely yellowish; M-150 . . . . . *Pontania* sp. 6.
- 20(19) Tenth abdominal tergum with distinct paired blackish or brownish markings . . . . . 21.
- 21(26) Ninth abdominal tergum without any markings or spots; antennæ with segment 3 sometimes incomplete . . . . . 22.
- 22(25) Tenth abdominal tergum with markings extending entire length and dumbbell-shaped; antennæ with segments 2 and 3 usually complete . . . . . 23.
- 23(24) Folded portion of leaf irregularly wrinkled; usually both edges folded; M-175. 1-1 . . . . . *Pontania* sp. 7.
- 24(23) Folded portion of leaf not irregularly wrinkled; usually one edge folded; Y-31-1-1, -8, 46(?) -2-2 . . . . . *Pontania* sp. 8.



- 25(22) Tenth abdominal tergum with markings not extending the entire length and not dumbbell-shaped; antennae with segments 2 and 3 incomplete; folded portion of leaf irregularly wrinkled; often both edges folded; Y-139-1-1. . . . . *Pontania* sp. 9.
- 26(21) Ninth abdominal tergum with some markings or spots; antennae with segment 3 usually complete. . . . . 27.
- 27(32) Ninth abdominal tergum with two transverse rows of minute colored spots. . . . . 28.
- 28(29) Tibia longer than femur; front concolorous with vertex; setae on abdominal terga more than three times as long as spiracles; Y-166-1-1. . . . . *Pontania* sp. 10.
- 29(28) Tibia subequal in length to femur; front not concolorous with vertex but darker; setae on abdominal terga less than three times as long as spiracles. . . . . 30.
- 30(31) Head blackish; mature larvae 9 mm. in length; on Salix; Y-8.46(?) -1-2. . . . . *Pontania* sp. 11.
- 31(30) Head brownish; mature larvae 11 mm. in length; on Populus; M-166. . . . . *Pontania* sp. 12.
- 32(27) Ninth abdominal tergum without two transverse rows of minute colored spots. . . . . 33.
- 33(34) Ninth abdominal tergum with two pairs of transverse blackish or brownish markings, interrupted on meson; head brownish with area along epicranial suture distinctly clear and paler; Y-142-1. . . . . *derosa* MacGillivray.
- 34(33) Ninth abdominal tergum with one pair of transverse blackish or brownish markings, interrupted on meson; head blackish or brownish in younger specimens, yellowish or light brown in older specimens with area along epicranial suture not distinctly paler. . . . . 35.
- 35(36) Tenth abdominal tergum with markings not reaching the paired caudal protuberances but broken on caudal half into minute spots; head yellowish with two minute brown spots on front; leaf-edge folder, folded edges not irregularly wrinkled; M-146. . . . . *Pontania* sp. 13.
- 36(35) Tenth abdominal tergum with markings reaching the paired caudal protuberances, not broken on caudal half into minute spots; yellowish or brownish without two minute brown spots on front. . . . . 37.
- 37(42) Ninth abdominal tergum with paired markings on its cephalic half. . . . . 38.
- 38(39) Ninth abdominal tergum with a transverse row of minute spots caudad of paired markings; leaf-edge-folder; both edges often folded and folded portion irregularly wrinkled; M-145. . . . . *Pontania* sp. 14.
- 39(38) Ninth abdominal tergum without a transverse row of minute spots caudad of paired markings. . . . . 40.
- 40(41) Antennae with segment 3 incomplete; only one edge of leaf-folded, folded portion not irregularly wrinkled; M-89,-147. . . . . *Pontania* sp. 15.
- 41(40) Antennae with segment 3 complete; both edges of leaf folded, folded portion irregularly wrinkled; M-116,-144. . . . . *Pontania* sp. 16.
- 42(37) Ninth abdominal tergum with paired markings on caudal half; antennae with segment 3 complete; single edge-folder, folded portion not irregularly wrinkled; Y-8.46(?) -2-2 (in part). . . . . *Pontania* sp. 17.

Nematid genus 1.—Larvae small, greenish; body cylindrical, tapering uniformly toward caudal end; segmentation distinct; annulation indistinct; third abdominal segment apparently with four annulets, annulets 1, 2, and 3 setiferous; thoracic legs conspicuously long, nearly as long as thorax, slender, with trochanter longer than femur; larvapods well developed, setiferous; tenth abdominal segment without the paired caudal protuberances; head circular, front flattened, smaller than thorax in width and

height; antennae with four segments, segments small, incomplete, with large sensory (?) pits, segments sometimes fused in part; spiracles not winged.

This genus is represented by a single unidentified species collected by Chester Young on *Salix* at Ithaca, New York. The larva is unique in the character of the legs in that the trochanter is longer than the femur. That this species belongs to the Nematinae is unquestionable but it is not closely related to any genus in particular except perhaps to *Pontania*. It may represent an undescribed genus.

Species 1.—Length, 10.5 mm.; body greenish; head brownish with dorsal half of front dark fuscous; labrum semicircular with slight mesal emargination; maxillary palpi with segment 1 nearly as long as segment 2 which is cylindrical and as wide at distal end as at proximal, segment 3 much smaller, segment 4 minute, peg-like, two distal segments curved mesad; galea conical, only slightly larger than labial palpi; thoracic legs with coxae subequal in length to tibiae, with trochanter slightly shorter than coxa, and as long on dorsal margin as on ventral, femur shorter than trochanter, cylindrical, three-fourths as wide as long, tarsal claws slightly curved; larvapods with 1-2 setae near cephalic aspect; setae slender, not stiff, rather sparse; tenth abdominal tergum rounded on caudal margin, with few setae; subanal lobe with several setae; abdominal segments with subspiracular areas with two setae and surpedal areas with a single setae; on *Salix nigra*; C-c.y.-77.

#### SUBFAMILY BLENNOCAMPINAE

Larvae (Figs. 19-20) moderately large; body subcylindrical, sometimes rather robust, tapering uniformly caudad, venter more or less flattened, usually distinctly spinose; segmentation distinct; annulation indistinct; third abdominal segment with five or six annulets, rarely apparently with four; thorax sometimes thickened; thoracic legs well developed, normal, tibia shorter than or subequal to femur; femur produced ventro-distad as pointed membranous projection; larvapods on segments 2-8 and 10, normal in form, glabrous, subsegmented, distal lobe truncate on distal margin and often curved mesad; tenth abdominal segment usually with several spines arranged in a transverse row along caudal margin; suranal and subanal lobes with several setae; head small, sparsely setiferous, narrower than thorax, front slightly convex; antennae with five segments, slender, elongately conical; ventral glands wanting; glandubae sometimes present; spiracles rarely winged; spines often very long, furcate, with two, three, or five branches, barbed, or represented by conical tubercles or sometimes reduced to short bifurcate tubercles; cuticle microscopically and densely spinulate; ultimate stage occurs, in which all setae and spines are lost and

body becomes colorless and glabrous; free leaf-feeders; sometimes gregarious.

The Blennocampinae as restricted by MacGillivray is a large subfamily rich in genera and species, and is related to Fenusinae and Scolionurinae. This is in agreement with Konow's statement altho this author makes his tribe Blennocampides the third in his subfamily Tenthredinini. Rohwer would group the majority of the genera under consideration in his subfamily Empriinae, but take out the genera Phymatocera and Tomostethus from the subfamily and place them in a subfamily by themselves. This arrangement has an advantage in classifying the larvae because of the fact that the larvae of Tomostethus lack the characteristic spines which readily distinguish the Blennocampinae from all other groups in the larval stages. The following key will separate the genera examined, with two additional ones, Erythraspides and Periclista, whose diagnostic characters are taken from Dyar's paper (1898b).

#### GENERA OF BLENNOCAMPINAE

- 1(2) Body without spines; with six annulets, annulets 2 and 4 each with a transverse row of minute but stalked glandubae. . . . . *Tomostethus* Konow.
- 2(1) Body with spines. . . . . 3.
- 3(10) Third abdominal segment with six distinct annulets; spines usually unbranched but conical, if branched, very short and minute, tenth abdominal tergum with small conical unbranched spines. . . . . 4.
- 4(7) Body spines conical and not bifurcate, blackish. . . . . 5.
- 5(6) Spiracles with distinct black wings. . . . . *Monophadnus* Hartig.
- 6(5) Spiracles without distinct black wings. . . . . *Hypergyricus* MacGillivray
- 7(4) Body-spines not conical but bifurcate, blackish or whitish. . . . . 8.
- 8(9) Spines whitish; tenth abdominal tergum not marked. . . . . *Blennocampa* Hartig.
- 9(8) Spines black; tenth abdominal tergum marked with black. . . . . *Erythraspides* Ashmead.
- 10(3) Third abdominal segment with five annulets, rarely apparently with four; spines in part usually bifurcate, long, never short and conical. . . . . 11.
- 11(12) Tenth abdominal tergum with a mesal spine cephalad of caudal marginal row of spines; subdorsal spines of prothorax with five branches; prothoracic spinal formula: 5-2-1:5:1-2; third abdominal segment: 2-2-2:0:3-2-2:2-1:1-2; ultimate tergum 1-1-1:2:2. . . . . *Monophadnoides* Ashmead.
- 12(11) Tenth abdominal tergum without a mesal spine cephalad of caudal marginal row of spines; subdorsal spines of prothorax with three branches at most. . . . . 13.
- 13(14) Second annulet of third abdominal segment with three spines dorsad of spiracular line; host-plants not confined to *Quercus* species; prothoracic spinal formula: 2-2-2:2-3:1-2; third abdominal segment 2-2-2:1:2-2-2:2-1:1:1. . . . . *Isodictium* Ashmead.
- 14(13) Second annulet of third abdominal segment with two spines dorsad of spiracular line; host-plants confined to species of *Quercus*; otherwise resembling the preceding genus. . . . . *Periclista* Konow.

#### TOMOSTETHUS KONOW

Larvae moderately large, length 17-21 mm., rather robust, yellowish white; body subcylindrical, tapering little caudad, venter flattened,



without spines, sparsely and microscopically setiferous; head black, shiny, much smaller than thorax; third abdominal segment with six annulets, annulets 2 and 4 each with a transverse row of few stalked glandubae; tenth abdominal segment without spines, truncate on caudal margin; spiracles not winged, but with a pair of faint ventral crescentic brown marks; antennae, (5, 4, 3), 2, 1 in older larvae and 5, (4, 3), 2, 1 in younger larvae; maxillary palpi, 4, 2, 1, 3, pointed; labial palpi rather slender, (1, 2); ultimate stage entirely whitish.

*Tomostethus bardus* Say.—Length, 18 mm.; width of head, 1.9 mm.; body whitish with yellowish tinge, in older specimens yellowish white; head shiny black with clypeus alone lighter in color; legs blackish brown; larvae gregarious; on ash; G-2, Y-8.14.

*Tomostethus multicinctus* Rohwer.—According to Sasscer's description (1911) the larvae of this species are indistinguishable from the preceding species but the bred adults have been assigned to this species by Rohwer. Larvae have not been examined.

#### BLENNOCAMPA HARTIG

Larvae rather small, length 15-20 mm.; greenish; body subcylindrical, slender, tapering uniformly caudad; spines small, bifurcate, tubercle-like or conical; head very small, third abdominal segment with six annulets, annulets 2 and 4 spinose; tenth abdominal segment spinose, spines conical, unbranched, numerous, arranged in four rows, 1: 1: 1-1-1: 1-1-1-1-1; typical prothoracic spinal formula: 2-2-1-1-1: 1-1-1: 1: 1-1; third abdominal segment, 2-2-1: 1: 2-2-1: 1-1-1: 1-1-1; antennae, 5, (1, 2, 3, 4); maxillary palpi, (2, 3, 4), 1, slender, pointed; labial palpi (1, 2), nearly equal to two distal segments of maxillary palpi taken together; legs with femur longer than tibia; larvapods normal in form, more or less rounded at distal end.

*Blennocampa spiraeae* Dyar.—Length, 16.5 mm.; width of head, 1.2 mm.; body greenish; head pale brown; legs concolorous with body; ocellar area entirely black, tips of mandibles and tarsal claws brown; maxillary palpi with segment 4 and labial palpi with segment 2 deep brown; prothoracic formula of spines variable, 2-2-1-1-1 or 2-3-1-1, or 2-1-1-1; abdominal segment on surpedal lobe with from 2-1 to 2-2 spines; tenth abdominal tergum with small, short, conical spines arranged in four rows as follows: (1) two pair of spines on each side of meson, (2) two spines on each side of the meson, near the center of the tergum, (3) lateral pairs sometimes with additional spines, and (4) the last and caudal row of five spines on each side of meson along the caudal margin of tergum, the three lateral spines closer together than the others; on *Spiraea*; not bred; M-28.



## ERYTHRASPIDES ASHMEAD

Larvae comparatively speaking small, inconspicuously spinose, greenish; third abdominal segment with five annulets, annulets 2 and 4 each with three minute bifurcate spines.

According to Dyar's Key (1898) the larvae of *Erythraspides pygmaeae* is distinguished from those of *Blennocampa spiraeae* by the black head and spines of the former. Record is meager, and without specimens no adequate diagnosis can be given.

## MONOPHADNUS HARTIG

Larvae rather small, length less than 15 mm., spotted; body rather robust, only slightly and uniformly tapering caudad; tubercles conical, small, blackish, not furcate; third abdominal segments with six annulets, annulets 2 and 4 tuberculate; tenth abdominal tergum with two rows of tubercles, some of which are bifurcate; prothoracic spinal formula: 1-1:1:1:1; third abdominal segment, 1-1-1:1:1-1-1:1:1; antennae 5, (4, 3, 2), 1; maxillary palpi (4, 2), 1, 3; labial palpi (1, 2); palpi rather thick and conical; spiracles with distinct black wings.

*Monophadnus nubilipennis* Norton.—Length, 14 mm.; width of head, 1.3 mm.; head blackish brown, clypeus alone lighter; body dirty white with yellowish tinge; legs grayish; on hellebore; Y-42,-8.42.

## HYPERGYRICUS MACGILLIVRAY

Larvae rather large and robust, spotted; length 16-20 mm., body subcylindrical, tapering but slightly and uniformly caudad; tuberculate, tubercles conical, short, stout, usually not furcate; third abdominal segment with six annulets, annulets 2 and 4 tuberculate; tenth abdominal segment with two rows of few tubercles; prothoracic spinal formula variable, but with a single tubercle on supraspiracular area and two tubercles ventrad of it; third abdominal segment also with variable number of tubercles, only two on subspiracular area; tubercles not furcate; spiracles with faint ventral crescentic brown marks but without definite wings; antennae rather obtusely rounded, segments decreasing in diameter from proximal to distal, but increasing in length; suranal and subanal lobes strongly convex, with numerous short recumbent setae; legs with femur distinctly longer than tibia; distal portion of femur dilated and produced ventro-mesad.

## SPECIES OF HYPERGYRICUS

Head black, genae, antennariae, ventral half of front and clypeus lighter in color; tubercles blackish; body whitish, faint grayish shade and yellowish tinge in older stages; legs grayish brown; antennae with segment 3 and 4 subequal in length; prothorax with spines, 2-2:1:1:1; third abdominal segment, 1-1:0:1-1:1:1; latus of body along supraspiracular lines with broken band of grayish shade, marks distinct and square

dorsad of each spiracle; on leaves and fruits of *Smilacina racemosa*; length, 18 mm.; width of head, 1.8 mm.; Y-73,-29-10,-8.73, M-181.....*sumipennis* Norton.

Head brownish yellow; length, 17 mm.; width of head, 1.9 mm.; spots on dorsum variable; body whitish with faint yellowish tinge; legs concolorous with body; supraspiracular lines without smoky-black band; prothoracic spines 1-1-1 or 1-1-1-1:1:1:1 or 3; third abdominal segment with 1-1; 1:1-1-1:1:1; any of the dorsal tubercles may be wanting; otherwise similar to the preceding species; Y; 20 specimens collected by Mr. J. R. Malloch on *Smilacina* in Illinois.....*Hypergyricus* sp. 1.

#### MONOPHADNOIDES ASHMEAD

Larvae small, distinctly spinose, greenish; length less than 17 mm.; body subcylindrical, tapering caudad, rather slender; spines furcate, with two, three, or more branches; third abdominal segment with five, apparently four, annulets, annulets 2 and 3 spinose; prothorax with spines, 5-2-1:(5 or 3):1:2; third abdominal segment, 2-2-2:0:(3 or 2)-2-2-2-1:1-2; tenth abdominal tergum with a mesal furcate spine cephalad of caudal marginal row of spines; legs rather slender, femur slightly longer than tibia, not dilated at distal end; spiracles unwinged; maxillary palpi, (1, 4), (2, 3); labial palpi, (1, 2); maxillary and labial palpi slender, pointed; antennae, 5, (1, 2, 3, 4), sharply pointed and slender; semigregarious.

*Monophadnoides rubi* Harris.—Length, 16 mm.; width of head, 1.6 mm.; head pale brownish green, distinctly setiferous, spines whitish, branches sometimes light brown; length of longer branches subequal to the width of head as seen in profile; tenth abdominal tergum with mesal spines with 2-3 branches, on the caudal third of the tergum cephalad of the marginal row of spines, sometimes another smaller unbranched spine cephalad of the furcate mesal spines; marginal row of spines, beginning with mesal spine, consists of two simple, one bifurcate and lower, and lateral simple spine on each side of meson; on *Rubus* and also on giant Ragweed; Y-8.17, M-19,-183, G-562, 500-3.

#### ISODYCTIUM ASHMEAD

Larvae rather small, usually distinctly spinose; length less than 17 mm.; body subcylindrical, tapering caudad, rather slender; third abdominal segment with five annulets, annulets 2 and 4 spinose, sometimes apparently four-annulate, with annulets 2 and 3 spinose; spines furcate, usually with two to three branches, branches usually conspicuously long, sometimes small, short, but always sharply pointed at distal end; spiracles never winged; thoracic legs normal, femur subequal in length to or longer than tibia; head blackish or spotted on vertex and front or uniformly greenish; spines on prothorax, 2-2-2-1:2-2:1:2; on third abdominal segment 2-2-2:1:2-2-1:1:1; tenth abdominal segment with a marginal row of spines, usually four on each side of meson.

Several species have been examined. None of the material has been identified altho the following larva may belong to *I. subgregarium*.

*Isodyctium* sp. 1.—Length, 15.5 mm.; head, 1.5 mm. wide; head marked on vertex and front with large confluent brownish spots, those on front sometimes separate; body uniformly greenish; legs concolorous with body, femur subequal in length to tibia; spines blackish, very long and furcate, with large proximal end, those ventrad of spiracular lines whitish; those one-half as long as head are wide as seen in profile; prothorax with spines, 2-2-2-1:2-2:1:2; third abdominal segment, 2-2-2:1:2-2-2:1-1-1; tenth abdominal tergum, 2-1:2:2, the mesal pair sometimes with confluent bases; maxillary palpi, (4, 2), 3, 1; labial palpi, 1, 2; ultimate stage: entirely whitish, vertex pale brown, third abdominal segment with five distinct annulets, setiferous but not spinose; on oak; M-6.

#### SUBFAMILY FENUSINAE

Larvae (Fig. 21) very small; body semicylindrical, venter flattened, depressed, tapering caudad, glabrous; segmentation distinct; annulation indistinct; third abdominal segment with either one or apparently 2-4 annulets; thorax slightly swollen, prothorax sometimes with dorsal and ventral shields; legs small, short, apparently with four segments, spreading cephalo-laterad; larvapods on abdominal segments 2-8, vestigial, merely mound-like; anal larvapods obsolete; tenth abdominal tergum glabrous without suranal processes or caudal protuberances, sometimes with small mesal projections; suranal and subanal lobes glabrous; head sparsely setiferous, depressed, subtriangular in outline, wedge-shaped in profile narrower than thorax and overlapped on caudal third by prothorax; vertical furrows wanting; antennae apparently with single segment; antacoria large; ocellaræ minute, located dorso-caudad of antennariae; ventral glands wanting; glandubæ wanting; spiracles indistinctly winged; cuticle sometimes with microscopic but distinct chitinated dentiform spines; larvae, leaf-miners.

The Fenusinae is a small subfamily represented by four genera in the Nearctic region. Systematists have always considered this group as closely related to the Scolioneurinae and Blennocampinae. MacGillivray is the only one who would assign them subfamily rank. Konow listed three European species, *dohrni*, *ulmi*, and *pumila*, under the old generic name *Kaliosysphinga*. The first two are now considered as types of distinct genera. They have been introduced into this country and are liable to do considerable damage at times. The genera studied are separable as follows:

#### GENERA OF FENUSINAE

Caudal end of body rounded, without a mesal suranal protuberance; sternum of ninth abdominal segment with a pair of swellings covered with distinct microscopic dentiform spines;



tenth sternum strongly convex, much shorter than ninth sternum .....

*Kaliofenusa* MacGillivray.

Caudal end of body truncate, with a mesal suranal protuberance; sternum of ninth abdominal segment flattened, uniformly and microscopically spinulate; tenth sternum slightly convex, nearly as long as the ninth sternum..... *Fenusa* Leach.

#### KALIOFENUSA MACGILLIVRAY

Larvae very small, greenish white; length less than 12 mm.; thorax broadest on mesothorax; declivous on dorsum from metathorax toward the head; head only slightly depressed, front convex; mouth-parts normal except labium, which is flattened; mandibles rather thick in profile; dorsum and venter covered with brownish, irregular, microscopic dentiform spines, larger on the center of segment and larvapods; caudal end of body rounded; tenth abdominal tergum without mesal protuberance; sternum of ninth segment with a pair of microscopically dentate swellings; tenth sternum strongly convex, much shorter than ninth sternum.

*Kaliofenusa ulmi* Sundevall.—Length, 10 mm.; width of head, .9 mm.; head light brown, legs brown, ocellaria, mandibles, maxillary palpi, deep brown; sternum of ultimate segment with transverse depression on the caudal third distinct; leaf-miners, on *Ulmus*, feeding on all tissues except upper and lower epidermis; Y-4-1,-4-2,-8.4.

#### FENUSA LEACH

Larvae very small, length less than 12 mm., greenish white; body rather uniform in width except at caudal end which tapers suddenly and distinctly; head strongly depressed; front flattened; mouth-parts protruding beyond the distal end of mandibles; body uniformly and microscopically spinulate; no distinct localized microscopic dentiform spines; caudal end of body truncate; tenth abdominal tergum with a distinct mesal conical suranal protuberance; sternum of ninth segment rather flattened, without microscopically dentate swellings; tenth sternum slightly convex, nearly as long as ninth.

*Fenusa dohrni* Tischbein.—Length, 10-11 mm., width of head, 1.1 mm.; head brown; prothorax with dorsal and ventral shields indicated; thoracic legs light brown, trochanter wanting, femur subequal in length to tibia; tibia with proximal end subequal in diameter to distal end of femur; tenth abdominal sternum with transverse depression in caudal fourth indistinct; body often greenish, green adipose tissues being visible thru the cuticle; dorsal vessel showing thru as light-colored line; leaf-miners on *Alnus vulgaris*, feeding habit similar to that of *Kaliofenusa ulmi*; Y-4. A, -43-1-2.



## SUBFAMILY SCOLIONEURINAE

Larvae (Fig. 22) very small; body semicylindrical, somewhat depressed, flattened on venter, broader on thorax, tapering caudad, glabrous, greenish, never with bright patterns; segmentation distinct; annulation indistinct, third abdominal segment with two annulets; larvapods rudimentary, mere swellings on abdominal segments 2-7, the anal pair adjacent on meson, forming a single protuberance; thorax thickened, prothorax often with distinct dorsal and ventral chitinized shields; thoracic legs small, slender, distinctly five-segmented, directed laterad; head depressed, subtriangular, wedge-shaped in profile, narrower than thorax; mouth-parts flattened and protruding, labium large, with submentum and mentum strongly chitinized; antenna one-segmented; vertical furrows usually wanting; tenth abdominal tergum abbreviated, glabrous; spiracles usually winged; glandubae obsolete; ventral glands wanting; cuticle often with minute dentiform tubercles; leaf-miners.

The Scolioneurinae is a small subfamily containing six genera, four of which are peculiar to the Nearctic region. All six genera are represented in the North American fauna. Prior to the recognition of the subfamily by MacGillivray, the species belonging to it were referred to the genera *Fenusa* and *Blennocampa*. Konow first segregated a species of *Entodecta* and later more of *Scolioneura* from *Blennocampa*, placing them, together with *Fenusa* and its allies, in other genera of his tribe *Blennocampides*. Rohwer would separate the genera of the Scolioneurinae from those of the *Blennocampinae* but unite them with those of the *Fenusinae* in the tribe *Messini* of his subfamily *Messinae*. The close affinity of the *Fenusinae* and *Scolioneurinae* is evident from the fact that all known larvae of these subfamilies are leaf-miners and that they possess similar types of structural modifications. The definitions here given are based on observations on two American species of *Metallus* supplemented by writings of European students—Cameron, Brischke, and Zaddach.

## METALLUS FORBES

Larvae small, length 10-13 mm., whitish or pale brownish; body depressed, rather stout, mesothorax broadest; pleuron of each segment tuberculate; cuticle with microscopic irregular chitinized dentiform tubercles, those on center of dorsum and venter largest; head directed ventro-cephalad, much narrower than thorax, attached to the ventral part of prothorax; vertical furrows wanting; front twice as long as wide, labrum subtriangular, small; antennae mamma-like; ocellaræ inconspicuous, about one-fifth the diameter of the antennaria; mouth-parts small but distinct, slightly modified; mandibular dentes sharp; maxillary palpi three-segmented, stipes elongate, galea digit-like, slightly curved

mesad and subequal in size to palpi, lacinia thin, small, plate-like; labium comparatively large, flattened; labial palpi inconspicuous, apparently 2-segmented; ligula globose and protruding; thoracic legs with coxa large, stump-like, following segments suddenly smaller and slender, trochanter ring-like, femur as long as wide, tibia longer than femur, cylindrical, chitinized, tapering gradually to distal end, tarsal claws broadly curved, sharp; mesothorax and metathorax with a dorsal membranous swelling on each side of the meson; spiracles distinctly and semicircularly winged; tenth abdominal tergum small, convex; anal setae wanting; subanal lobe small, prominently convex.

#### SPECIES OF METALLUS

Head brownish, not concolorous with body, epicranial suture very distinct; dorsal and ventral shields distinct and brown; dorsal shield transverse, covering dorsum of prothorax, proventral shield very large, occupying entire venter between prothoracic legs caudad of and continuous with brown cervacoria, mesoventral and metaventral shields small, transverse, triangular between legs; labium with submentum strongly chitinized, brown with dark carina on meson and along caudal margin, mentum brown, longer than wide; larvopods with crescentric brownish band on cephalic aspect; length, 11-12 mm.; on Rubus; Y. .... *rubi* Forbes.

Head pale or whitish, concolorous with body, at least not distinctly colored; dorsal and ventral shields obsolete, only rarely faintly indicated; labium with submentum broad and without dark median longitudinal carina, depression on meson rarely present, never dark and distinct; larvopods without crescentric brownish band on the cephalic aspect; length, 10 mm.; on Rubus; Y. .... *bethunei* MacGillivray.

The larvae of *Metallus rubi* were described by Forbes, but the original specimens are apparently lost. The description given here is based on specimens in the Cornell Collection. Forty-three larvae of *M. bethunei* were examined thru the courtesy of Mr. H. G. Crawford of Guelph, Ontario, Canada.

#### SUBFAMILY HYLOTOMINAE

Larvae (Fig. 23) moderately large; body semicylindrical, venter flattened, distinctly wider than high, widest on abdominal segments 1-3, tapering caudad, caudal segments only one half the width of widest segments; yellowish green, spotted or not; segmentation distinct; third abdominal segment with three annulets, all setiferous, often tuberculate; thoracic legs large, spreading laterad, apparently six-segmented inclusive of claws; claws sharply curved, large, distinctly separated from fifth segment by suture and with a large pulvillus-like swelling; larvopods setiferous, on abdominal segments 2-6 and with rudimentary 7th pair, or on 2-7 and 10 with rudimentary 8th pair; antennae one-segmented, either conical or button-like, if conical, larvopods on abdominal segments 2-6 and 10; spiracles distinctly winged; glandubae obsolete; tenth abdominal tergum without suranal processes.

The Hylotominae in the adult stage is closely allied to the Schizocerinae, but in the larval stages their affinities, if extant, are not so manifest. The larvae are peculiar in possessing six-segmented thoracic legs and varying numbers of larvapods. The shape and general appearance of the larvae are so characteristic that they alone are sufficiently reliable for identification in the field. Two genera are represented in the Nearctic region, the genus *Atomacera*, which includes only a few species, has not been studied.

#### HYLOTOMA LATREILLE

Head, conspicuously shiny black, brown or yellowish, or with a brown median streak; body with minute blackish tuberculate setiferous spots forming interrupted longitudinal rows along some or all of the subdorsal, latero-dorsal, supraspiracular, subspiracular, and pedal lines; annulation usually 2, 3, 1; annulet 1 with a few minute setae, annulets 2 and 3 with a transverse row of a few stiff brown setae together with very minute setae scattered around the larger setae; subspiracular tubercles obsolete; pedal area prominent, produced laterad and oblique, extending entire length of segment; maxillary palpi normal, four-segmented, segment 1 flattened, with distinct mesal projection, segments 2 and 3 cylindrical, segment 4 minute, peg-like; labial palpi normal, three-segmented; larvapods located close together near the meson, proximal portion chitinized, setiferous, distal portion small, membranous, non-setiferous, bluntly rounded, those on seventh or eighth abdominal segment lacking membranous distal portion.

The genus is divisible into two sections by the structure of antennae and number of larvapods. Owing to the incompleteness of published records of larvae of this genus, involving in some cases confusion in specific identification, it is not possible to determine many of the specimens collected. The following key will separate the species represented in the collections studied.

#### SPECIES OF HYLOTOMA

- 1(10) Antennae distinctly conical or peg-like, twice as long as wide; larvapods on abdominal segments 2-6 and 10, seventh segment with rudimentary pair; head always uniformly blackish, brownish, or yellowish; body always with numerous minute blackish spots arranged longitudinally along subdorsal, dorso-lateral, supraspiracular and pedal lines. ....2.
- 2(5) Head always black, thoracic legs with all segments blackish; tenth abdominal tergum blackish. ....3.
- 3(4) Tenth abdominal segment on ventral half blackish; area between larvapods with minute colored spots; area ventrad of pedal folds with minute spots; latus of each segment with a few very minute secondary setiferous spots besides regular tuberculate spots; on *Crataegus* Y-194-3 194-2; on *Prunus*? Y-194-5. . . .*Hylotoma* sp. 1.
- 4(3) Tenth abdominal segment on ventral half unmarked, whitish; area between larvapods without minute colored spots; area ventrad of pedal folds without minute spots;



- latus of each segment without minute setiferous spots; on *Alnus*: Y-194-4. ....  
*Hylotoma* sp. 2.
- 5(2) Head not always blackish but usually yellowish or brown; thoracic legs not with all segments blackish, segments distad of coxa usually brownish or brownish yellow; tenth abdominal tergum not always blackish. .... 6.
- 6(7) Head blackish; tenth abdominal tergum yellowish; subanal lobe yellowish; spots between larvapods numerous and brownish; latus of each segment with many very minute secondary setiferous spots; tuberculate spots of body yellowish with brown border; on oak; Y-214-1-2. .... *Hylotoma* sp. 3.
- 7(6) Head yellowish or reddish brown; tenth abdominal tergum blackish; subanal lobe whitish. .... 8.
- 8(9) Area ventrad of pedal folds with many minute setiferous spots; area between larvapods sometimes with spots; spots on body not uniformly blackish or brownish but blackish on cephalic and also usually on caudal portion of the body those on middle portion brownish or yellowish with brown border sometimes spots all pale yellowish brown; head reddish or yellowish brown; on *Crataegus*; Y-222. ....  
*scapularis* Klug.
- 9(8) Area ventrad of pedal fold without spots; area between larvapods never with spots; spots on body uniformly blackish or brownish; head yellowish or yellowish brown; on elm; C-C.U. 668 Y-29-24. .... *Hylotoma* sp. 4.
- 10(1) Antennae button-like, usually wider than long; larvapods on abdominal segments 2-7 and 10, eighth segment with rudimentary pair; head blackish brownish or with a distinct median streak from occiput to front; body sometimes not spotted except on each side of the meson on cephalic segments. .... 11.
- 11(14) Head blackish or brownish; body distinctly and regularly spotted; tenth abdominal tergum and subanal lobe usually blackish; thoracic legs usually with coxae blackish or brownish and other segments brownish or grayish. .... 12.
- 12(13) Tenth abdominal tergum and subanal lobe whitish; all colored areas or spots of body brownish; area between larvapods with few setiferous spots; area ventrad of pedal fold with many setiferous spots; on *Salix discolor*; C-Young 61. .... *Hylotoma* sp. 5.
- 13(12) Tenth abdominal tergum and subanal lobe blackish or brownish; all colored areas or spots blackish or brownish; area between larvapods usually without setiferous spots; area ventrad of pedal fold with varying number of spots; on *Prunus*; Y-1946-1 G-Onekama No. 23; Maine 1915; C-C.U. 656 C.U. sub. 64. .... *Hylotoma* sp. 6.
- 14(11) Head yellowish or light brownish with brown streak along epicranial stem; body not regularly and distinctly spotted except along dorso-meson on cephalic segments; tenth abdominal tergum never blackish or brownish; thoracic legs always concolorous with body; Y-185-1-2 (*Azaëa*) Y-185 (*Willow*) M-113 (*birch bred*) M-108 (*hazel*). .... *macleayi* Leach.

## SUBFAMILY SCHIZOCERINAE

Larvae (Fig. 24) small; body subcylindrical, flattened on venter, tapering caudad, mesothoracic and metathoracic segments somewhat swollen, prothorax distinctly tapering cephalad; whitish or creamy white, never spotted or striped; segmentation and annulation indistinct; third abdominal segment with three annulets, all annulets provided with a transverse row of tubercles; spiracles on annulet 1; tenth abdominal tergum without suranal or caudal protuberances; larvapods on abdominal segments 2-8 and 10, the venter of ninth segment with a pair of minute



protuberances; thoracic legs modified, prothoracic legs apparently four-segmented, distal segment pad-like, tarsal claws wanting; mesothoracic and metathoracic legs apparently three-segmented, distal segment pad-like with a sharp claw on cephalic side; antennae apparently one-segmented, segment large with several clear spots; antennaria ventrad or slightly caudad of ocularium; spiracles winged; glandubae obsolete; in younger specimens larvapods sometimes very indistinct; tubercles often indistinct; leaf-miners.

The Schizocerinae is represented in the Nearctic region by a single genus, *Schizocerus*, and includes a limited number of species. Modern systematists have always associated this subfamily with the Hylotominae, the two being separated by the presence or absence of the free part of  $Sc_2$  in the front wing. The larvae of this subfamily are unique in having thoracic legs and maxillary and labial palpi modified by reduction in the number of segments.

#### SCHIZOCERUS LEPELETIER

Larvae small, length less than 15 mm., creamy-whitish; head small, pale brown, higher than wide, sparsely and microscopically setiferous; annulation 1, 2, 3; annulets above spiracular lines with tubercles, 2 on annulet 1, four on annulet 2, and three on annulet 3, annulet 1 with a row of tubercles on venter; a row of tubercles between larvapods and surpedal area; subspiracular area not tuberculate or warty; tenth abdominal tergum small, only slightly convex, tubercles almost obsolete, with several stiff short setae on caudal margin; venter of ultimate segment with distinct anal larvapods, subanal lobe with a pair of long and short tubercles on each latero-caudal margin; maxillary palpi apparently three-segmented, distal segment very minute, formula, 2, 1, 3; labial palpi apparently two-segmented; mandibles as viewed from side narrow and slender; totaglossa of labium large; spiracles winged, wings small, oblong; spiracular line dividing the *latus* into two subequal dorso-ventral parts.

*Schizocerus zabriskiei* Ashmead.—Head pale brownish-green, body whitish; in younger specimens head brownish, body with minute tubercles touched with brown; legs, and venter between legs brownish; tubercles ventrad of surpedal area and dorsad of larvapods usually three in number in mature larvae and two in younger larvae; mature specimen, length, 13 mm.; width of head, 1.3 mm.; on *Portulaca*; Y, G.

*Schizocerus* sp. 1.—Larvae indistinguishable from the preceding species. This species was collected at Muncie, Ill., by Dr. Edna Mosher, who bred adults. It is considered by Dr. MacGillivray to be a new species.

## SUBFAMILY ACORDULECERINAE

Body (Fig. 25) subcylindrical, tapering caudad, venter flattened, thorax distinctly swollen; segmentation distinct; annulation indistinct, third abdominal segment with apparently three annulets, all annulets tuberculate, setiferous; thoracic legs 5-segmented, spreading laterad, distal segment consisting of a sharp recurved claw and caudal membranous globose swelling; prothoracic legs one-half as large as metathoracic; larvapods rudimentary on abdominal segments 2-7 and 10, increasing in size from cephalic pair to sixth pair; tenth abdominal segment truncate, small, without suranal processes; antennae flattened, apparently 1-segmented; abdominal segments 2-4 or 2-5 and 8 with crescentic sucker-like protuberances, one on each postsubspiracular protuberance; ventral glands wanting; spiracles not winged; glandubae wanting.

The Acordulecerinae, according to MacGillivray (1906), is represented on the North American continent by a single genus, *Acordulecera*. Rohwer would divide the subfamily into two tribes, Acordulecerini and Conocoxini, the former including besides *Acordulecera*, *Pantherix* and possibly *Thulea* and the latter *Conocoxa* and *Nithulea*. A radically different arrangement is that of Konow who regarded *Acordulecera* as one of fourteen genera included in his tribe Lobocerotides which was one of four tribes constituting his subfamily Lophyrini. Konow seems to have been unfamiliar with the larvae of the Nearctic genus *Acordulecera*, for he speaks of the larvae of Lophyrini as "mit 16 Abdominalbeinen; an Coniferen."—a characterization not at all applicable to the genus under consideration. The host-plant of two species of *Acordulecera* have been recorded, and one species recognized in the larval stage. I have examined larvae of several unbred species.

## ACORDULECERA SAY

Larvae very small, length less than 12 mm., greenish, never spotted or striped; head usually brownish or pale; annulation, 3, (2, 1); prothorax constricted; annulets with transverse row of slight tubercles, each bearing slender peg-like setae; lateral lobes distinct; tenth abdominal tergum with several setae; suranal and subanal lobes with several setae; maxillary palpi rather slender, uniformly tapering distad; mandible thick; labial palpi small; ligula dilated, rounded; free leaf-feeders; gregarious.

## SPECIES OF ACORDULECERA

- 1(4) Sucker-like protuberances on abdominal segments 2-5 and 8. .... 2.
- 2(3) Head with vertex blackish brown, front distinctly lighter in color; legs whitish concolorous with body; sucker-like protuberances with three marginal setae; length 9.5 mm.; width of head 1.2 mm.; on butternut; Y-8.93(?) 2-2... *Acordulecera* sp. 1.
- 3(2) Head with vertex light brown, epicranial stem deep brown, front sometimes deep brown; in young specimens head entirely dark brown; legs brown; sucker-like

- protuberances with three marginal setae; length 11 mm.; width of head 1.3 mm.; on chestnut and butternut; Y-93 C-cu 667.....*Acordulecera* sp. 2.
- 4(1) Sucker-like protuberances on abdominal segments 2-4 and 8.....5.
- 5(8) Sucker-like protuberances with three marginal setae; on oak.....6.
- 6(7) Head light brown with epicranial stem deep brown or brownish with vertical furrows lighter in color; legs brownish; length 9 mm.; width of head 1.2 mm.; Y-131 -137, C-cu 680, M-37.....*Acordulecera* sp. 3.
- 7(6) Head yellowish or light brown, with epicranial stem concolorous with body; length, 7 mm.; width of head, 1.1 mm.; M-239, M-243, C-y11.....*dorsalis* Say.
- 8(5) Sucker-like protuberances with five marginal setae; head deep brown, vertical furrows and epicranial arms lighter in color; legs whitish, concolorous with body; length, 9 mm.; width of head, 1.2 mm.; on hickory; Y-144-5.....*musta* MacGillivray.

#### FAMILY PAMPHILIIDAE

Larvae (Fig. 1) of medium size; body subcylindrical, slightly flattened on the ventral aspect; sublateral lobe on the ventro-lateral margin distinct, moderately large; body slender to robust; segmentation and annulation distinct; cuticle microscopically setiferous, appearing smooth, often delicate, transparent; color usually greenish or creamy white; head semi-globose, prominent, as wide as thorax; color creamy or brownish or blackish; mouth directed ventrad; head completely exposed, sparsely setiferous; epicranial suture and vertical furrows present; antennae extremely long, setaceous, conspicuous, seven-segmented; ocellaria located ventro-laterad of antennariae; mouth-parts normal, sericos produced and prominent; prothorax with shield-like, usually brownish, broad patches on the dorsal and lateral aspects; thoracic legs modified, setiform, sharply pointed, segments cylindrical, distal segment very long, slender, straight; third abdominal segment with four annulets on dorsal and ventral aspects; spiracles on the second annulet; larvapods wanting; eighth abdominal segment on the venter mesad of the lateral lobe with a fleshy protuberance resembling a larvapod, ninth segment cylindrical, smaller than the preceding; tenth segment depressed, rounded on the caudal margin, usually setiferous, sometimes conspicuously so, often with colored patches, always with a median hook-like suranal process near the caudal margin of the tergum; subanal lobe with a pair of setiform, three-segmented conspicuous subanal appendages; insects one- or two-brooded; spinning silken web or rolling leaves for their nests; solitary or gregarious; pupate in the ground.

The Pamphiliidae is an easily circumscribed family of eight or nine genera and a large number of species which are peculiar to the Northern hemisphere. The adults differ from all other Hymenoptera except the Xyelidae in the preservation of the subcostal vein in the hind wings. In this character it is more generalized than the Xyelidae altho it is more specialized than this family in other features of venation. Brischke



and Zaddach (1865) discussed the immature stages and biology of eleven European species of the Pamphiliidae and pointed out that certain of their habits may be of taxonomic significance. The larvae of these species fall into one or the other of two groups according to the type of nests they build. The first group contains those whose larvae build nests by tying the leaves of their food-plants together with threads of silk and are either solitary, as *Lyda*, or gregarious, as *Cephaleia* and *Neurotoma*. The second group consists of those whose larvae build nests by rolling the edge of the leaves of their food-plants and live inside the tubes so formed, as *Pamphilius*. Some of this latter group make portable nests out of detached pieces of leaves, as *Pamphilius inanitus* on *Rosa*. The adults, however, are so closely related to each other that Rohwer (1911) considered such a subdivision impractical. Konow (1901), in his analytical table of the larvae, included sixteen species, representing four genera, but did not register any Nearctic species. According to this writer (1905) the larvae of *Lyda* and *Cephaleia* feed on coniferous plants while those of *Neurotoma* and *Pamphilius* attack deciduous plants. Nothing is known concerning the biology of Anoplolyda. Dyar (1895) included in his table ten Nearctic pamphilids but, excepting *Pamphilius ocreatus*, all were unidentified and many were taken from descriptions given by Packard (1890).

Of about fifty-five Nearctic species representing seven genera, *Acantholyda*, *Itycorsia*, *Cephaleia*, *Caenolyda*, *Neurotoma*, *Pamphilius*, and *Anoplolyda*, only five species have been identified in the larval stage, and the food-plants of about six species recorded.

Four identified and several unidentified species have been examined. It is not possible to define the genera with this limited material; the species studied can be separated as follows.

#### SPECIES OF PAMPHILIIDAE

- |       |   |                          |
|-------|---|--------------------------|
| 1(14) | Subanal appendages with the second segment longer than or subequal to the third segment, never distinctly shorter; head usually dark-colored; tenth abdominal tergum with colored patches. ....   | 2.                       |
| 2(3)  | Subanal appendages with the second segment subequal in length to the third, all segments black; first segment longer than the two distal segments taken together; head black; body olive-green with yellowish lateral lobes; on spruce; Packard (1890)-35. .... | <i>Pamphiliid</i> sp. 1. |
| 3(2)  | Subanal appendages with the second segment longer than third, the third usually darker in color than the others; first segment longer than or nearly equal to the two distal segments taken together; head dark brown to green. ....                            | 4.                       |
| 4(5)  | Head green; tenth abdominal tergum without colored patches; body green; subanal appendages with the second and third segments black; on <i>Pinus strobus</i> ; Packard-83. ....   | <i>Pamphiliid</i> sp. 2. |
| 5(4)  | Head not green, usually brownish; tenth abdominal tergum with or without colored patches; body not greenish, sometimes reddish or olivaceous; subanal appendages usually with segments brownish; on <i>Pinus</i> and <i>Abies</i> . ....                        | 6.                       |



- 6(13) Head brown to yellowish.....7.
- 7(12) Head dark brown.....8.
- 8(9) Head paler along epicranial arms; subanal appendages with first segment as long as all the other segments taken together; all segments pale to light brown; length, 25 mm.; width of head, 3 mm.; body robust, large; following parts dark brown: head except along epicranial arms, prothoracic shields, thoracic surpedal lobe, coxae, sterna between thoracic legs, cervical sclerites, markings on the tenth abdominal segment, median suranal process, and antennae; ocellaræ black; suranal process short and erect; tenth abdominal tergum with a pair of lateral patches, not connected along caudal margin; tenth abdominal sternum with a median brown patch, distinctly rounded on cephalic margin; subanal appendages light brown, first segment equal in length to other two taken together, segment 2 longer than 3; thoracic legs with fifth segment as long as fourth, and third taken together; antennal formula: (2, 5), 3, 6, 1, (4, 7); cuticle distinctly reticulate, each area brownish; three specimens in MacGillivray collection bearing label "Cephalæia sp. No. 839? Maine." (The identification is open to question, but, since these larvae are readily distinguished from the larvae of *Pamphilius* and *Neurotoma* by the characters used in the table here, they may be considered, tentatively at least, as representing the genus *Cephalæia*.).....*Cephalæia* sp. 1.
- 9(8) Head not paler along epicranial arms, but uniformly brownish.....10.
- 10(11) Head pitch-brown; body pinkish to reddish brown; on spruce; Packard-36.....*Pamphiliid* sp. 3.
- 11(10) Head horny brown; body horny brown; subanal appendages with first segment longer than other two taken together, third segment brown; on *Pinus strobus*; Packard-84.....*Pamphiliid* sp. 4.
- 12(7) Head yellowish to brownish yellow; body pale brick-red or yellowish, each segment with a large reddish spot on the spiracular line; subanal appendages with first segment nearly equal in length to other two taken together; all segments blackish; on *Pinus strobus*; Packard-85.....*Pamphiliid* sp. 5.
- 13(6) Head pale red, with a black spot on the front; body reddish olive-green with purplish meso-dorsal line; on Austrian pine; closely related to *Lyda campestris*; Packard-82.....*Pamphiliid* sp. 6.
- 14(1) Subanal appendages with the second segment distinctly shorter than the third; head variously colored, blackish to pale; tenth abdominal tergum either with or without colored patches.....15.
- 15(18) Tenth abdominal tergum with a colored patch on each side, median triangular patch between the cephalic ends of the lateral patches wanting; lateral patches connected along the caudal margin of tergum; sternum with a large colored patch.....16.
- 16(17) Head blackish or dark brownish, in younger specimens pale brown; subanal appendages with first segment longer than other two segments taken together, third longer than second, all segments brown, the third darker; cervical sclerites pale brown, dorsal and lateral shields of prothorax pale to light brown, patches on the ultimate segment brownish; body with a pink dorsal line on the meson; antennae in mature specimens with formula, (2, 3, 5), 1, 7, (4, 6); ocellarum about one-third the diameter of antennaria; ocellaræ small, eccentric, near the mesal margin of ocellarum; mouth-parts brownish; length, 19 mm.; width of head, 1.9 mm.; on wild cherry; G.....*Neurotoma fasciata* Norton.
- 17(16) Head lighter in color, yellowish, sometimes brownish yellow; subanal appendages with first segment nearly equal to other two taken together, all segments black; following parts blackish: prothoracic shields, thoracic legs, markings on ultimate segment, subanal appendages, ocellaria, thoracic sterna; the black markings of tenth abdominal

- tergum connected along the caudal margin; black marking of tenth sternum large, completely covering the sternum, and with its cephalic margin between the subanal appendages straight; antennae with formula, (3, 5), 2, 1, 7, (6, 4); length, 18 mm.; width of head, 1.7 mm.; on plum; G. . . . . *Neuroloma inconspicua* Norton.
- 18(15) Tenth abdominal tergum either with a colored patch on each side and with a median triangular patch between the cephalic ends of the lateral patches always present, the lateral patches sometimes not connected along the caudal margin of the tergum, the sternum with a large colored patch; or the tergum without colored patches and the sternum either with a pair of small round spots or without markings. . . . . 19.
- 19(22) Tenth abdominal tergum with two lateral triangular patches and one mesal patch and sternum with a large colored patch. . . . . 20.
- 20(21) Head blackish; body greenish-white; subanal appendages with the first segment longer than the other two taken together, all segments pale brown, the third sometimes darker; following parts blackish: head uniformly, antennae, prothoracic shields, thoracic lateral lobe, markings on ultimate segment, suranal hook, cervical sclerites, and coxae; antennae with formula, (3, 2), 5, 1, 7, (4, 6); eighth uromere with a pair of marginal ventral glands near caudal portion of the sublateral lobe, both pale brown; in life, body glossy white with diffused fleshy-reddish tint; antennae and subanal appendages whitish; length, 19 mm.; width of head, 1.9 mm.; on Cornus; nests made by rolling edges of leaves cut across from the margin to the midrib; gregarious; Y-125. . . . . *Pamphilus* sp. 1.
- 21(20) Head light brown, with a black spot on the apex of front; subanal appendages with the first segment nearly equal in length to the other two taken together, two proximal segments creamy, third deep brown; body whitish green; ocularia brown, a black spot at the origin of the epicranial arms; following parts brown: thoracic shields, cervical sclerites, and markings on the ultimate segment; tenth abdominal tergum with a median cephalic triangular patch between the lateral patches; subanal appendages with second segment longer than half the length of the third; thoracic legs pale or creamy; antennae, beyond the first segment, deep brown, with formula: (2, 3, 5), 1, 7, (4, 6); length, 19 mm.; width of head, 1.8 mm.; on blackberry; G. . . . . *Pamphilus dentatus* MacG.
- 22(19) Tenth abdominal tergum without colored patches. . . . . 23.
- 23(26) Tenth abdominal sternum without a pair of small colored patches. . . . . 24.
- 24(25) Head uniformly pale brown; subanal appendages with the first segment as long as other two taken together, the second shorter than the third, all segments pale brown; ocularia large, about one-third the diameter of antennaria, black; following parts blackish brown: narrow prothoracic shields, cervical sclerites, and antennae; suranal hook brown without colored base; antennae with formula, (2, 3), 5, 1, 7, (4, 6); length, 12 mm.; width of head, 1.5 mm.; host unknown; Y-163-3. (This species closely resembles *P. persicus* MacG.). . . . . *Pamphilus* sp. 2.
- 25(24) Head not uniformly pale brown, vertex brown, front with a brown spot; subanal appendages with the first segment as long as the other two taken together, distal two segments brownish; following parts brown: prothoracic shields, cervical sclerites, antennae, and suranal process; legs pale brown, darker in young specimens; length, 17 mm.; width of head, 1.8 mm.; on blackberry; M-69. . . . . *Pamphilus* sp. 3.
- 26(20) Tenth abdominal sternum with a pair of small colored patches; head pale to light brown, front sometimes with a brown spot, usually without it; subanal appendages with the first segment nearly equal in length to other two taken together, the second segment shorter than the third, all segments pale to brownish; ocularia and mandible at distal end blackish brown; suranal process brown with its base pale; antennae

brown; tenth abdominal sternum with small brown round spot on each side; length, 16 mm.; width of head, 1.6 mm.; larvae solitary, leaf-edge rollers on Cornus; M.

*Pamphilius ocreatus* Say.

#### FAMILY CEPHIDAE

Body (Fig. 2) cylindrical, sometimes slightly depressed, enlarged at thorax, slightly and uniformly tapering caudad, slender or moderately stout; segmentation usually distinct; annulation sometimes indistinct; cuticle smooth or verrucose, microscopically and very sparsely setiferous; color generally pale or creamy white, never with distinct bright marks; head circular in contour, semiglobose, moderately large, narrower than thorax, caudal portion concealed by prothorax, pale brown or concolorous with body, sparsely setiferous; mouth-parts directed ventrad, normal in form, brownish; antennae with four or five segments, conical; ocellaræ small, with ocellaria less than one-fifth the diameter of antennaria and located latero-caudad of it; epicranial suture and vertical furrows present; mesothorax distinctly, and metathorax with dorsal and lateral aspects somewhat swollen; thoracic legs vestigial, fleshy, mamma-like, tarsal claws wanting; third abdominal segment with two or three annulets, sometimes indistinct; venter with three annulets; larvapods wanting, sometimes with slight swellings in normal position of larvapods; lateral lobes prominent, extending the entire length of the segment; tergum of ultimate segment with mesal longitudinal broad depression and distinct suranal process; sternum of ultimate segment with a pair of inconspicuous vestigial, papilliform subanal appendages ventrad of the cephalic end of the anal slit; internal feeders, boring into the stem of monocotyledonous and herbaceous plants and bushes; pupation in tunnels in the host-plants.

The Cephidae contains about fourteen genera and is moderately rich in number of species, some of them of intercontinental distribution. Nine genera are represented in North America. Practically all systematists have considered this group as a distinct aggregate worthy of family rank. Rohwer (1911), however, has expressed the opinion that future studies may possibly make it advisable to unite this group with the Xyelidae and to treat each of them as subfamilies. There have so far been no facts or reasons brought to light which call for such a step. On the other hand, MacGillivray's study has emphasized the fact that "so far as the wings are concerned, they (Cephidae) are the most distinct of any group of the Tenthredinoidea, and are only indirectly related to any of the other families." They are generalized in the manner of the origin of media but are specialized in other features of the wings. On the basis of larval characters this family is related to the Pamphiliidae and is quite unrelated to the Xyelidae.

The systematic position of the osculant genus *Syntexis* is unsettled. In the original description Rohwer (1915) stated that this genus has



affinities with both the Cephidae and Xiphydriidae and on the basis of venation, it probably belongs to the latter as defined by MacGillivray. Certain features other than venation, however, led Rohwer to place it in the Cephidae. It is not safe to venture any opinion without careful examination of the larvae, but their antennae and their lack of papilliform subanal appendages suggest close affinity with the Xiphydriidae.

At least six out of sixteen American species have been recognized in the larval stages and their host-plants recorded. *Janus integer* and *Cephus cinctus* are economic pests. Konow's tribe Macrocephides includes the species whose larvae bore into the pith of shrubs and woody twigs, and his tribe Cephides embraces those whose larvae bore into the stalks of Graminaceae.

Middleton (1917) published descriptions and keys for distinguishing the larvae of five species representing four genera, *Adirus*, *Janus*, *Cephus*, and *Hartigia* together with a definition of the groups based on "characters common to all the genera studied and probably to the family." He reserved for future discussion the question of the systematic position of the Cephidae, but pointed out the obvious affinity of this group with the Siricidae on one hand and the Pamphiliidae on the other. Gahan (1920) described the larva of *Trachelus tabidus* (Fab.) and added a key for separating this larva from that of *Cephus cinctus* and *C. pygmaeus*.

#### GENERA OF CEPHIDAE

- |       |   |                          |
|-------|---|--------------------------|
| 1(10) | Papilliform subanal appendages present on the ultimate abdominal segment. . . . .   | 2.                       |
| 2(3)  | Suranal process depressed on the distal portion, oval in cross-section, with strongly chitinized dentiform tubercles on the proximal portion; antennae five-segmented.  | <i>Janus</i> Stephens.   |
| 3(2)  | Suranal process not depressed on the distal portion, circular in cross-section, with or without strongly chitinized dentiform tubercles on the proximal portion; antennae four-segmented. . . . .   | 4.                       |
| 4(5)  | Suranal process proximad of distal cylindrical portion with strongly chitinized dentiform tubercles. . . . .  | <i>Adirus</i> Konow.     |
| 5(4)  | Suranal process proximad of distal cylindrical portion without strongly chitinized dentiform tubercles. . . . .   | 6.                       |
| 6(7)  | Terga of eighth and ninth abdominal segments setiferous, each with a transverse row of distinct setae; tenth abdominal tergum as viewed from side strongly convex and truncate on the caudal aspect; suranal process with stiff setae not arising from distinct chitinized bases. . . . .   | <i>Trachelus</i> Jurine. |
| 7(6)  | Terga of eighth and ninth abdominal segments glabrous, each without a transverse row of distinct setae; tenth abdominal tergum as viewed from side not strongly convex and not truncate on the caudal aspect but gradually declivous caudad; suranal process with stiff setae arising from distinct chitinized bases. . . . .                                     | 8.                       |
| 8(9)  | Suranal process with distal chitinized portion very short and ring-like, or very long and cylinder-like, more than twice as long as wide; suranal process with a single transverse row of setae proximad of the distal chitinized portion or with two or more whorls of setae; the distal margin of the distal chitinized portion not distinctly serrate. . . . . | <i>Cephus</i> Latreille. |



- 9(8) Suranal process with distal chitinized portion, as long as wide, cylinder-like; suranal process proximad of the distal chitinized portion with two or more whorls of setae; distal margin of the distal chitinized portion minutely but distinctly serrate. . . . .  
*Hartigia* Schiodte.
- 10(1) Papilliform subanal appendages on the ultimate abdominal segment wanting.  
*Syntexis* Rohwer.

Should *Cephus* and *Hartigia* (Middleton, 1917) and *Trachelus* (Gahan, 1920) prove to possess five-segmented antennae, as reported, contrary to the observations of the present writer, the genus *Janus* can be separated from them by the chitinized dentiform tubercles and *Trachelus* by the glabrous eighth and ninth abdominal terga.

#### JANUS STEPHENS

Antennae distinctly with five segments; segments 1 and 2 short, ring-like, segment 3 longer, but half as wide as segment 1, segment 4 cylindrical, longer than wide, segment 5 elongate-conical, twice as long as wide, subequal in length to or shorter than segment 4; suranal process short, strongly chitinized, nearly as long as wide at proximal end, dentiform tubercles with circular rows of stiff setae on the proximal half, distal half small, depressed, narrowly oblong in cross-section; subanal appendages peg-like, with a minute seta at the distal end, apparently segmented, without setae near the proximal end; lateral area of suranal lobe with 2-3 setae; mandible with four dentes.

#### SPECIES OF JANUS

- Subanal appendages distinctly two-segmented, segment 1 ring-like, much larger in diameter than segment 2; antennae with segment 5 about one-half as long as segment 4; bores in *Salix* and *Populus*. . . . . *abbreviatus* Say.
- Subanal appendages indistinctly two-segmented, segments subequal in diameter; antennae with segment 5 subequal in length to or only slightly shorter than segment 4; bores in *Ribes* species (currant); *C*. . . . . *integer* Norton.

#### ADIRUS KONOW

Antennae distinctly with four segments; segment 4 long, peg-like, bluntly pointed, nearly three times as long as wide, twice as long as segment 3; suranal process large, distal fourth strongly chitinized, suddenly constricted, circular in cross-section, with chitinized dentiform tubercles; subanal appendages peg-like, fleshy, apparently unsegmented, with setae near the proximal end, these setae separated from the remainder of the setae on the sternum; lateral area of suranal lobe with 20-28 setae.

*Adirus trimaculatus* Say.—Middleton has described the larvae in detail. They bore in the stems of blackberry and rose. Thru the kindness of Dr. E. P. Felt, one mature and two young damaged specimens from

the New York State Museum, labeled "a 2766" and "a 2261" were examined by me.

#### TRACHELUS JURINE

Antennae apparently with four segments—according to Gahan five segments present; body thickest dorso-ventrad in mesothorax, second and third abdominal segments widest, the ninth and tenth tapering suddenly; suranal process rather short, tapering caudad gradually, chitinized dentiform tubercles wanting, with or without stiff short setae, if setae present they do not arise from chitinized bases; ultimate tergum setiferous on both sides of the median depression, convex as viewed from side, truncate on the caudal aspect, not declivous caudad; third abdominal segment with three annulets, annulet 2 largest and with a transverse row of setae; subanal appendages peg-like, unsegmented.

*Trachelus tabidus* Fabricius.—Suranal process without distinct constriction, with or without brownish setae, if present, setae arranged in a irregular circle in the proximal half; subanal appendages brownish with 2 minute setae at the distal end, and with 1 or 2 setae which are separated from the remainder of the setae on the sternum; lateral area of suranal lobe with 5-7 setae; antennae with segment 4 bluntly rounded, segments 2 and 3 ring-like, segment 1 narrow but large in diameter with a seta on the dorsal margin, segments all brown; bore in the stalks of wheat, rye, and barley (Gahan 1920).

#### CEPHUS LATREILLE

Antennae apparently with four segments—according to Middleton five segments present—segment 4 less than twice as long as wide; abdominal segments 5-8 with ventral swellings corresponding in position to larvapods; suranal process without chitinized dentiform tubercles, either with a narrow ring-like distal chitinized portion and a semicircular row of setae or with a long cylindrical distal portion and two or more irregular rows of whorls of setae on the proximal portion, the distal margin of the distal chitinous portion entire and smooth; subanal appendages papilla-like, cylindrical, more than twice as long as wide, bluntly rounded at the distal end, with one or more setae near the proximal end; lateral area of suranal lobe with 7-15 setae; mandible with three dentes.

According to Rohwer (1917) only two species of this genus are known to occur in North America. They can be separated as follows:

#### SPECIES OF CEPHUS

Suranal process with the distal chitinized portion cylindrical, twice as long as wide, setae on the proximal portion arranged in two or three irregular whorls; subanal appendages with several setae; lateral area of suranal lobe with about 15 setae; the only true Nearctic species known; bores in stalks of *Elymus*, *Agropyron*, *Phleum*, and wheat. *cinctus* Norton.

Suranal process with distal chitinized portion ring-like, shorter than wide, setae on the proximal portion arranged in a semicircular row on the dorsal aspect; subanal appendages with one or rarely two setae, lateral area of suranal lobe typically with seven setae; introduced from Europe; bores in stalks of wheat. . . . . *pygmaeus* Linnaeus.

#### HARTIGIA SCHIODTE

Antennae apparently with four segments—according to Middleton (1917) with five segments—segment 4 longer than segment 3, elongate, conical; suranal process twice as long as wide at proximal end, without strongly chitinized dentiform tubercles, with several whorls of spinous setae; subanal appendages two-segmented, sometimes segmentation indistinct, with accompanying setae separated from the remainder of setae of the sternum; lateral area of suranal lobe with 15-20 setae.

*Hartigia cressoni* Kirby.—The larvae of this species have been described in detail by Middleton. They bore in the stems of *Rubus* in California. The preceding generic definition was based upon specimens obtained thru the courtesy of Mr. Harry S. Smith, of Sacramento, California, and does not quite agree with that given by Middleton (1917).

#### FAMILY XIPHYDRIIDAE

Larvae (Fig. 3) small; body subcylindrical, thorax and two caudal segments distinctly swollen; segmentation distinct; annulation obsolete; creamy white, no markings; glabrous; thoracic legs rudimentary, fleshy, mamma-like, without tarsal claws; larvapods wanting; ultimate segment with distinct suranal process, without subanal appendages; ocellaræ wanting; mouth-parts modified; maxillary palpi apparently two-segmented; antennae apparently with three segments; metaspiracles functionless, very much smaller than abdominal spiracles; cuticle on dorsum smooth, on venter microscopically, sharply, and densely spinulate; tenth abdominal tergum with deep meso-dorsal depression; wood-borers.

The Xiphydriidae contains four genera, *Derecyrtia*, *Brachyxiphus*, *Xiphydria*, and *Konowia*, which may be divided into two groups on the presence or absence of the radial cross-vein in the wings. Systematists have generally considered this group as a subfamily of the Siricidae, but MacGillivray (1906) has elevated it to its present standing on the venational characters, which he has proven to be the most generalized of the specialized Tenthredinoidea. Rohwer (1911) would divide the family into two subfamilies, Xiphydriinae and Derecyrtinae, the latter being monobasic. Of the four genera, two are represented in the Nearctic fauna.

In a recent synopsis of the Nearctic wood-wasps, Rohwer (1918b) tabulates eight species of *Xiphydria*. He considers that *X. walshii* Westwood, which MacGillivray (1916) assigned to the genus *Konowia* belongs to the original genus, although the species was unknown to him, and states that "it is possible that it is *provancheri* Cresson." Rohwer suggests



that the specimens which Patten (1878) reared from *Betula nigra* and regarded as *X. attenuata* Norton do not belong to this species but are similar to an undescribed female bearing a Bradley manuscript name. Nothing is known concerning the immature stages of *Konowia basalis* Say. The larvae of *Xiphydria* are wood-borers and confine their attacks to dead and decaying wood of deciduous trees. European species infest willows, poplar, elm, and birch, and American species, maple, hickory, and birch. Konow (1901) listed four species, *Xiphydria prolongata*, *X. camelus*, *X. longicollis*, and *X. abdominalis* in his key to the larvae of Tenthredinoidea.

#### XIPHYDRIA FALLEN

Larvae comparatively small; thorax distinctly swollen, the meta-thorax being the largest segment of the body; abdominal segments 1-2 cylindrical, subequal in diameter; third abdominal segment with a single annulet; two caudal segments somewhat globose; sublateral lobe moderately large, extending the entire length of the segment; suranal process comparatively long, with dentiform tubercles near the base; tenth abdominal sternum much smaller than the tergum; head and ultimate segment with long setae; head semiglobose, vertical furrows present; epicranial suture in part indistinct; antennariae distinct; antennae three-segmented, segments 1 and 2 ring-like, segment 3 conical, longer but of much smaller diameter than the preceding segments; labium very small, without median emargination; mandibles with distinct dentes; maxillae with small modified palpi, apparently two-segmented; galea conical, smaller than palpi, lacinia fleshy, tubercle-like, with several setae; labium with submentum and mentum large, convex, membranous, palpi apparently with three segments, small, median lobe large, flattened on venter, suboblong; spiracles large, oblique, not winged; glandubae wanting.

*Xiphydria provancheri* Cresson.—Length, 12 mm.; width of head, 1.6 mm.; body yellowish white; head creamy white; mouth-parts brownish; suranal process arising from large brownish strongly chitinized suranal lobe, deep brown, at proximal end, more than twice as long as wide, distal two-thirds suddenly and distinctly smaller in diameter than proximal third, with two circular rows of dentiform tubercles and setae on the proximal third and two distinct ventral dentiform tubercles on the distal third, one caudad of the other, these without setae; on birch.

This description is based upon a rare specimen collected at Saranac Inn, New York State, Aug. 20, 1900, and generously loaned by Dr. E. P. Felt. The larva bores into partly decayed heartwood of standing birch and makes a gallery about 2.5 mm. in diameter. The burrows are invariably filled with the borings, except a short curved portion thru which the adult makes its way to the surface. A parasite, *Pammegischia xiphydriae* Ashmead, was reared by Dr. Felt from larvae of this species.



Dr. Felt (1906) also found another larva making moderately large cylindrical burrows in decaying birch and considered it as probably belonging to *X. attenuata*. He refers to the rearing of this species by Patton and suggests *Rhyssa humida* Say as its parasite. Since the identity of Patton's specimen is questioned and since the adult was apparently not reared, it is not possible to identify the specimen under consideration. If it were really *X. attenuata*, then it should be known as *X. abdominalis* as proposed by Konow (1905) and Rohwer (1918).

#### FAMILY SIRICIDAE

Body large, 30-40 mm., cylindrical, uniform in diameter thruout (Fig. 4), fleshy, plump; integument smooth, transparent, non-setaceous, light in color; head circular, half as high as thorax; mouth directed ventrad, mostly exposed, but slightly overlapped by prothorax; antennae inconspicuous, apparently one-segmented; ocellaræ wanting; epicranial suture wanting and vertical furrow indistinct; mouth-parts not normal in form, light in color; prothorax large; mesothorax and metathorax short in comparison with abdominal segments; legs rudimentary, mamma-like, subequal in size, borne on fleshy conical lobes; larvapods wanting; typical segment with two indistinct annulets, sublateral lobe distinct but not prominent; tenth abdominal segment semiglobose in profile; tenth tergum distinctly depressed by a median furrow; suranal lobe on the meson with dark colored, chitinized, suranal process; subanal appendages wanting; internal-feeder, bores in the trunks of deciduous and evergreen trees.

The Siricidae contains five genera and about fifty species, most of which are confined to the northern hemisphere. The recognition of the fact that these insects constitute a well-circumscribed group dates back to the time of Linnaeus (1758) who described five species of Siricidae among those of his heterogeneous genus *Ichneumon*, three of the five having become the types of three modern genera. Systematists have universally agreed in considering this group worthy of family rank. The family falls into two natural divisions, Siricinae, including three genera, *Sirex*, *Urocercus*, and *Xeris*, and Tremecinae, embracing two genera, *Tremex* and *Teredon*. The genus *Xeris* was associated with the genera composing the Tremecinae both by Ashmead (1898) and Konow (1905), but Rohwer (1911) proposed a more natural arrangement, placing this genus in the Siricinae. Bradley (1913) definitely divided the two groups on the number of segments of labial palpi and the retention of cerci in the adults.

According to Bradley (1913) there are twenty species reported for North America, representing all the known genera. The specific characters of some common species, as *Sirex nigricornis*, *Urocercus cressoni*, and *Tremex columba*, are subject to a wide range of variation and several varieties have been described. So far as known, the larvae of the Siricinae

are wood-borers attacking conifers, those of the Tremecinae boring in deciduous trees. *Tremex columba*, or three races of this species which infest maple, elm, apple, pear, beech, oak, and sycamore, are the best-known examples. The food-plants of only three American species are known, these including *Sirex cyaneus* and *Urocerus albicornis*. Larvae of the Siricinae have not been examined.

#### TREMEX JURINE

Larvae conspicuously large; body cylindrical, slightly flattened on the venter; large, robust, usually bare except on head and tenth abdominal segment; whitish or creamy white; setae microscopic; head semiglobose, slightly wider than high on cephalic aspect, semicircular in profile, produced to the ventral half of the front, then suddenly truncated, pale brownish; mandibles and coilae deep brown; antennae apparently one-segmented, conical; antacoria partly chitinized and bearing a few small setae; ocellaræ wanting; depression mesad of antennaria which is sometimes called the "eye" is a pretentorina; vertical furrows concealed by overhanging prothorax; clypeus small, light in color; labrum transverse, convex, thick, asymmetrical, without median emargination, but with a notch on the right third of slightly oblique cephalic margin; mandibles strong; mandacuta distinct, brown; mandibularia narrow, inconspicuous, maxilla fleshy except subgalea, stipes large; palpi two-segmented, small; galea conical, brown, small, arising from broad shoulder which bears a few tiny setae on the lateral portion; lacinia round, lobe-like, bearing three rows of brown setae, which decrease in length on cephalic or dorsal side; labium compact, submentum narrow, transverse, membranous, mentum convex, lobe-like, deeply emarginate on cephalic margin, ligula round, fitting into the emargination of mentum, palpi small, two-segmented, second segment much smaller than first, conical and brown, sericos large, transverse, distinct, crescentic; prothorax large, produced dorsad and cephalad, overlapping the caudal third of the head; mesothoracic and metathoracic segments about one-half the length of abdominal segments except the first abdominal which is only little longer than the metathorax; thoracic legs rudimentary, mamma-like, short, tipped with tiny chitinized spot, borne on fleshy conical pedal lobe; cervical sclerites wanting; sternum with transverse subtriangular lobes which meet on the meson in front of median lobe between and slightly cephalad of prothoracic legs; metaspiracles as large as abdominal spiracles; abdomen slightly and uniformly tapering to the caudal end; annulation indistinct on dorsum, apparently with but one annulet, the venter with two annulets, the second annulet larger than the first; sublateral lobe prominent, extending the entire length of segment as a single oblique elevation; spiracles large, brown; ninth abdominal segment a little shorter than the eighth; tenth

tergum convex, lateral area of suranal lobe broad, suranal process prominent, deep brownish, strongly chitinized, compressed, with two pairs of small but distinct teeth.

The foregoing definition of the genus is based on one species, *Tremex columba*.

*Tremex columba* Linnaeus.—Length, 40 mm.; width of head, 4 mm.; ultimate segment with setae as follows: tergum near the caudal margin on each side of the median furrow with a small, brown, sharp, hook-like spine, with tiny setae which arise from large calices; ventral side of suranal lobe with such setae; tenth sternum small; small brown spot at the lateral end of anal slit; subanal lobe non-setiferous; subanal appendages wanting; I-8396; G-.

The eggs of the Pigeon Tremex are oblong-oval, pointed at both ends about 1.2 mm. in length, deposited singly, but in limited area, close to each other; oviposition takes place in early summer, female sometimes fails to withdraw ovipositor and dies *in situ*; larvae on hatching in the wood make a gallery and feed for probably one season; transformation takes place in the burrow; adults emerge thru circular hole, about 8 mm. in diameter. The larvae are parasitized by *Thalessa lunator* and also by *Megarhyssa atrata* Fabricius, according to Champlain (1921).

Felt (1906) suggests as remedial measure against this insect, the cutting down and burning of all trees badly infested. Keeping the trees in vigorous health is supposed to be sufficient to prevent injury as the larvae work only in weakened or partly decaying wood.

#### FAMILY MEGALODONTIDAE

Antennae long, conspicuous, multisegmented, located above or near the ocellaræ; larvapods wanting; last abdominal segment rounded, with a pair of bristle-like segmented subanal appendages; larvae feed on herbaceous plants.

This family contains four genera, Rhipidioceros, Megalodontes, Melanopus, and Tristactus, and about thirty-five species, which are distributed in Europe, Asia, and North Africa. Systematists have invariably associated this family with the Pamphiliidae, but that this position is unnatural has been conclusively shown by MacGillivray. He has pointed out that it represents a line of specialization very similar to that found in the Siricidae, and that while it is more closely related to this family than to any other, an abundance of characters justify one in considering it as a distinct group.

Only one species, *Megalodontes spissicornis* Klug has been recognized in the larval stage. The larvae, according to Hiendlmayr (1878), are found on *Lasperpitium latifolium* L. in central Europe from the end of July to



the beginning of August. In the younger stages, they are gregarious and live in a common nest like many Pamphiliidae, but they spin an individual web when half-grown. There is one generation a year.

This interesting species was not available for study, and the foregoing definition is abstracted from Konow (1901) and may be found by later students of little value in defining the family. This family, so far as the recorded larval characters are concerned, seems to be closely associated with the Pamphiliidae in possessing the bristle-like subanal appendages and long conspicuous antennae. Future observations, however, may possibly reveal more important characters, not given in the brief synopsis of Konow.

#### FAMILY ORYSSIDAE

Body (Fig. 5) eruciform, grub-like, subcylindrical, slightly depressed, swollen in the middle of the abdomen, tapering at each end; segmentation distinct; annulation obsolete; creamy white, without colored markings; spiracles on prothorax and first eight abdominal segments; thorax increasing in size caudad, thoracic legs obsolete; larvapods wanting; fourth abdominal segment largest in diameter, size of segments decreasing rapidly caudad, last segment smallest; suranal process and subanal appendages wanting; head white, compressed cephalo-caudad, circular in frontal contour, narrower than thorax; antennae with a single segment, papilla-like; mandibles tridentate; maxillae and labium vestigial, fleshy, lobe-like, without palpi; ocellaræ wanting; larvae parasitic on wood-boring larvae of Coleoptera; pupation in the pupal cells of the hosts.

The Oryssidae contain six genera and a limited number of species distributed thruout the world. The genus *Oryssus* alone is represented in the Nearctic region. In former years the family has been associated with the Siricidae, but recently writers are in accord in regarding it as an extremely specialized compact group. MacGillivray (1906) came to the conclusion that "so far as their wings are concerned the presence of the second anal cell in the front wings is the only structure that would place the genus *Oryssus* in the superfamily Tenthredinoidea"; The group is not only highly specialized in the adult characters but a recent discovery of the parasitic habit of the larvae isolates these Hymenoptera from all other Tenthredinoidea as a unique class. In fact Rohwer and Cushman (1917) have gone so far as to propose a new suborder, *Idiogastra*, placing it "intermediate between the suborder *Chalastogastra*—where adult would place it—and the suborder *Clistogastra*—with which the larva would ally it." Whether this arrangement is acceptable or not, the fact that this group is remarkably well circumscribed and that it represents the summit of an extremely isolated line of specialization in the Tenthredinoidea can not be doubted.



Only one species, *Oryssus occidentalis* Cresson, has been recognized in the immature stages. The definitions given here are based on the descriptions and figures of this species published by Rohwer and Cushman (1917). It is quite possible that future studies may prove them inadequate for the identification of the larvae of other genera and species yet to be discovered.

#### ORYSSUS LATREILLE

Larvae small; epicranial suture faint, arms obsolete; clypeus crescentic, narrow; fronto-clypeal and clypeo-labral sutures distinct; labrum more than twice as wide as long, with shallow mesal emargination; antennaria distinctly elevated, antacoria extensive, mound-like; antennae small, mamma-like; mandibles strongly chitinized, curved, narrow mesal dentis larger than lateral dentes, these subequal in size, sharp; maxillae fleshy, subtriangular, unsegmented lobes; annulation on dorsum indistinct, with apparently two annulets, venter with one; sublateral lobes distinct, extending the entire length of the segments; spiracles visible from dorsal aspect; segments transversely raised and with a few minute tubercles.

*Oryssus occidentalis* Cresson.—Color white with mandibles and chitinized ridges near the mouth brown; head one-third as wide as the widest segment of the body—the fourth abdominal segment; maxillae with minute brownish spots bearing about three sensory papillae; labium with about four stout setae on each side of meson; prothorax declivous toward the head, forming straight line with the latter in profile, on dorsum subequal in length to mesothorax; metathorax half as long as mesothorax; lengths of abdominal segments as follows: 8, (1, 9), (2, 7), (4, 6), 5, 10 on dorsum, (6, 7, 8), 5, 1, 3, (2, 4), 9, 10 on venter, 8, 7, 4, (1, 2, 5, 6), 3, 9, 10 on latus; tenth abdominal segment one-fourth as wide and one-third as high as the fourth and sixth segments respectively; dorso-cephalic margin of mesothoracic and eighth abdominal segments distinctly, and of metathoracic and abdominal segments 5, 6, 7, 9, 10 slightly convex, and of abdominal segments 2 and 3 concave; ventro-cephalic margin of abdominal segments 1, 6, 7, 8 distinctly, and of 2 and 9 slightly, concave, of 3, 4, and 5 convex, of 1 and 6 with a distinct convex emargination on each side of meson; abdominal segments with the distance from spiracles to dorsal surface uniform on lateral aspect and much shorter than the distance from spiracles to the ventral surface, the latter variable and increasing caudad to the sixth segment and diminishing thereafter; “each thoracic and abdominal segment has dorsally at each side of the middle a low, transverse elevation surmounted by a transverse row of four or five short, stout back-pointing spines”; setiferous elevations on abdominal segments 1-7 and 9 and on metathorax near the caudal margin of the segments, those of prothoracic

and mesothoracic and eighth abdominal segments being in the middle; tenth abdominal segment with small pointed protuberances directed caudad; venter of segments with brownish spots in place of legs; larvae parasitic on the larvae of *Buprestis confluens* Say, *B. laevis* Le Conte, and possibly other species of Buprestidae.

#### IV. PHYLOGENY

A classification based on phylogeny is one of the essential concerns of philosophical taxonomy. In order to ascertain the genetic relationship of organisms, synthetic as well as analytic, consideration of evidence drawn from all the branches of biological science is imperative. The indissoluble relation of morphology, embryology, and paleontology to taxonomy is so manifest and familiar that no comments are needed. The time has come, however, when a critical examination of the phylogenetic significance and the taxonomic value of the physiological and biological attributes of animals must be made. Whatever evidence comparative physiology, biochemistry, and genetics may offer should be incorporated as far as possible with the data obtained in other more commonly exploited fields of research. Only in this way is it possible to arrive at a comprehensive, systematic and complete summation of knowledge of animals. This is the primary function of philosophical taxonomy, and in this sense the saying of W. S. Jevons that "science can extend only so far as the power of accurate classification extends," is true.

There are good reasons to believe, however, that even to-day morphology, as of old, holds its supreme place in systematic investigations as it offers fundamental assistance in determining the genetic affinities of organisms. The success of a study of phylogeny based on morphological evidences depends on the ability of the investigator to select the proper structures, to determine the direction and nature of changes undergone by these structures, and to draw legitimate conclusions by judicious interpretation of the facts observed. Data obtained from studies of the external anatomy of the larval stages of entometabolous insects are of necessity incomplete of themselves for determining the phylogeny of the group; yet, in the absence of other means of approach to the problem, they constitute essential facts significant enough to merit careful consideration.

The opinions of scientists in regard to the systematic importance of the characters based upon the immature stages of Entometabola have been divided. There are some who ascribe no importance whatsoever to them and entirely ignore this phase of taxonomy. There are others who recognize the importance of the larvae from the viewpoint of synoptic classification as they are primarily interested in the practical purpose of

synoptic descriptions and keys. There are still others who believe in the intrinsic importance of the immature stages in the study of phylogeny. The reasonableness of the oft-repeated objection which was voiced by Comstock (1918) that the larvae of insects exhibit a cenogenetic development and, therefore their ontogeny bears little or no relation to the phylogeny of the race, must be admitted in regard to certain structures which are entirely too adaptive and too much modified by environmental factors in meeting the trophic requirements of particular species or genera. But admission of this fact is not incompatible with a belief in palingenesis of other structures. Besides, the warning that the cenogenetic peculiarities, which may be of value as distinguishing characters, are of no phylogenetic significance and must, therefore, be judiciously and discriminately distinguished from more important palingenetic characters, applies not only to the classification of the larvae but to the taxonomy of the adults as well. This objection alone does not invalidate a belief in the intrinsic importance of the immature stages from the phylogenetic point of view. While the writer does not minimize the danger of a too confident expectation of finding phylogenetic indices in the successive ontogenetic stages in entometabolous insects, yet he is equally reluctant to abandon his hope in regard to the taxonomic value of the characters of immature insects. The present study is a partial justification of his contention.

Students of the Tenthredinoidea have recognized the practical importance of the larvae in determining the systematic position of different taxonomic units. Norton (1867) stated that "Mr. Walsh has shown that in some species of *Euura* and *Nematus* bred by him, it was almost impossible to detect any difference in the imago, while the larvae varied greatly. Doubtless our opinion will be greatly modified by future discoveries." Cameron (1882) was of the opinion that the larvae were of great value in differentiating the tribes and subtribes altho they appeared to be of little use in regard to the genera. MacGillivray (1913) goes further and states that "it was hoped from a study of the immature stages of the Tenthredinoidea that some information might be obtained as to the validity of the species based on obscure anatomical details." Rohwer also often uses the characters of the larvae as collateral evidence in deciding the systematic position of certain subfamilies and genera.

Nothing definite is known in regard to the ancestors of the Hymenoptera beyond the probability that they have somehow arisen from a primitive type of some neuropteroid-like Palaeodictyoptera. The order is considered to be one of the most, if not the most, highly specialized of all insects. Systematists are unanimous in regarding the Tenthredinoidea as the most generalized of the Hymenoptera. It is difficult, if not impossible, to conjecture the primitive larval type of the Tenthredinoidea. Judging, however, from what are universally considered to be generalized



conditions in insects in general and in the Tenthredinoidea in particular, the probable ancestral type of larva may be characterized as follows: body cylindrical; segmentation distinct; annulation indistinct, annulets few in number; head exposed, subglobose, distinct from the trunk; thorax and abdomen more or less similar in structure excepting the three pairs of thoracic legs, which are well developed and consist of five segments, tarsal claws distinct; abdomen with twelve segments including the telson; larvapods present on abdominal segments 1-10; antennae long, composed of several segments; ocellaræ present, one on each side of head; mouth-parts well developed, maxillary and labial palpi segmented; tenth abdominal tergum without caudal protuberances or suranal process; eleventh abdominal sternum with a pair of segmented subanal appendages; ten pairs of functional spiracles present, including metaspiracles; larvae free leaf-feeders.

There are, as was pointed out by Comstock (1893), two kinds of characters of phylogenetic importance. "First, characters indicating difference in kind of specialization; and second, characters indicating difference in degree of specialization of the same kind. The former will indicate dichotomous divisions of lines of descent; the latter merely indicate degrees of divergence from a primitive type."

In determining the probable genetic affinities of the families of the Tenthredinoidea, the following structures have been taken into consideration: thoracic legs, larvapods, subanal appendages, ocellaræ, antennae, mouth-parts, suranal process, and metathoracic spiracles. The list does not by any means exhaust the structures which might be employed for this purpose, but it is believed that the structures listed offer the most reliable and essential basis for the determination of a phylogeny based upon larval characters. The significant changes in these structures are: addition or reduction of parts; difference in degrees of development of existing parts; and modifications in length, size, shape, and degree of chitinization of the parts. These modifications have been interpreted according to the Comstockian principles quoted above.

The thoracic legs are among the most persistent structures in the adult and larval stages of insects in general, and their absence is unquestionably an indication of specialization by reduction. It is likewise reasonable to assume that any modification of the typical, simple, cylindrical, five-segmented condition as regards the form or the number of segments is a sign of specialization. The legs of the larvae of the Pamphiliidae approximate most closely the primitive condition in the number, shape, and structure of the segments. The tarsal claw is straight and very slender. In the Xyelidae the legs assume a condition different from that of the Pamphiliidae. The differentiation of segments in size and shape has proceeded further and the tarsal claws have become distinctly claw-

like. The legs are very small compared with the size of the body. The Tenthredinidae present a series of conditions which illustrate beautifully cases of modification both by reduction and addition. The typical, well-developed, five-segmented legs undoubtedly represent the normal sequence in development from the condition found in the Xyelidae. The apparently six-segmented condition of the Hylotominae, four-segmented legs of the Fenusinae, and three-segmented condition of the Schizocerinae, together with the development of distal fleshy lobes in the first- and last-named subfamilies are cases of specialization. The fact that the specialization by reduction of segments has not proceeded at the same rate in the last two subfamilies is indicated by the difference in the structure of the segments. It is interesting to note that the prothoracic legs of the Schizocerinae still retain four segments in spite of the fact that in the two caudal pairs the number of segments has been reduced to three. The osculant genus *Phlebotrophia* is unique among all other Tenthredinidae in having the legs modified to such an extent as to lose all resemblance to normal segmented legs. They have become mere fleshy, indistinctly segmented, clawless protuberances. In this character this genus resembles highly specialized families such as the Cephidae and its allies. The Cephidae, Xiphydriidae, and Siricidae represent a series of modifications in which the changes have resulted in fleshy, vestigial, entirely clawless legs with or without indication of segmentation. Judging from the size and degree of segmentation, the Xiphydriidae is more generalized than the Siricidae and more specialized than the Cephidae. The Oryssidae is entirely apodous, and the fact that it is parasitic on buprestid larvae leaves no doubt as to its extreme specialization.

The larvapods are considered as true appendages of the abdominal segments. Their presence is highly significant from a phylogenetic point of view. The larvae of the Tenthredinoidea are divisible into two types according to the presence or absence of the larvapods. The Xyelidae and Tenthredinidae represent the type with polypodous larvae and the other five families represent the type with apodous larvae. In the first group the Xyelidae possess the maximum number, or ten pairs, of larvapods, while the Tenthredinidae are provided with six to eight excepting certain specialized genera which possess very vestigial or no larvapods. It has not been possible to determine the reason for the invariable absence of larvapods upon the first and ninth uromeres in the Tenthredinidae. It may be that the same mechanical factors which have caused the fusion of anal larvapods in boring larvae like *Caulocampus* are also responsible for this condition. The size and, to some extent, the structure and position of the larvapods vary within the Tenthredinidae as in the Schizocerinae, Hylotominae, and Fenusinae. It is interesting to note that the gall-making genus *Pontania* retains normal larvapods as well as thoracic legs, while the

leaf-miners have both thoracic and abdominal legs reduced in the number and size of their segments. The small size and reduced number of segments are correlated with the well-developed thoracic legs of the Hylo-tominae. In this subfamily the claws are very large, sharply curved, and provided with empodia-like distal structures, indicating a great adaptation for clinging to leaves. This fact is sufficient to account for the reduction of the larvapods. The Pamphiliidae and four specialized families in the same line of development are entirely without larvapods. It is highly desirable to determine whether this apodous condition signifies a common origin of all five families. Upon this question hinges much of the interpretation of the phylogeny of the Tenthredinoidea.

In characterizing the larvae of the hypothetical primordial Tenthredinoidea the abdomen was considered as provided with the maximum number of appendages, including ten pairs of larvapods and a pair of subanal appendages. This assumption is based upon the fundamental fact that the progenitor of insects having evolved from a typical arthropodan organism possessed the typically arthropodan character, abdominal appendages. This assumption is justifiable in view of the following facts: (1) the possession of appendages on all of the abdominal segments is a fundamental arthropodan characteristic; (2) the embryos of practically all insects exhibit at some time during their development rudiments of abdominal appendages; (3) appendages are present on all or some of the abdominal segments in the postembryonic stages of the Apterygota; (4) the gonapophyses of the Exometabola represent the true abdominal appendages in this group of insects; (5) the larvapods and other appendages are present in the larvae of the Mecoptera, Lepidoptera, generalized Hymenoptera, and, possibly, in some other orders,—all these facts indicating the wide occurrence and fundamental continuity of abdominal appendages in the Hexapoda. It is, therefore, not unreasonable to assume that the progenitor of insects, at least in some stage of its development, possessed appendages on all of the abdominal segments. The same argument supports the contention that the ancestors of the Hymenoptera undoubtedly closely resembled the remoter ancestors of the Insecta. The larvae of the progenitor of the Hymenoptera for this reason have been considered as provided with the maximum number, or ten pairs, of larvapods, a pair on each of the first ten abdominal segments and a pair of subanal appendages on the eleventh abdominal segment. If this assumption is true, the larvae of the Xyelidae, which possess ten pairs of larvapods, must be considered as representing the most primitive condition found in the Hymenoptera. Graber (1890) has shown that in the larvae of *Hylotoma* the larvapods arise from the embryonic limb-rudiments and are directly evolved from them during the development and, therefore, the larvapods are the true appendages of the abdomen, homodynamous



with the thoracic legs and homologous with the abdominal appendages of generalized insects. There is no reason for considering the larvapods of the Xyelidae as embryologically and morphologically different from those of *Hylotoma*, consequently the larvapods of the Xyelidae must be the true appendages of the abdomen; and since the larvae of this family are provided with the maximum number of larvapods, they must be considered as the most generalized of the Tenthredinoidea. The Tenthredinidae with six to eight pairs of larvapods and certain other morphological and biological characters are unquestionably related to the Xyelidae and probably represent a line of evolution from a xylelid-like ancestral stock. Among the Tenthredinoidea with apodous larvae, the Pamphiliidae, with a pair of segmented subanal appendages, is undoubtedly the most generalized of all five families. The origin of the Pamphiliidae is consequently an important question. For the reasons already stated in connection with the larvapods, the progenitor of the Hymenoptera has been considered as possessing a pair of subanal appendages on the caudal segment of the body. In this character as well as in all others the Pamphiliidae approach most nearly the primitive condition and, except for the absence of larvapods, unquestionably represents the most generalized condition found in the Tenthredinoidea, outranking even the Xyelidae. The loss of larvapods in this case is just as difficult to explain as the loss of subanal appendages in the case of the Xyelidae. These structures, the larvapods and subanal appendages, must have been lost during the course of phylogeny since the progenitor undoubtedly possessed both of these structures, and these two families, in spite of their generalized conditions, must represent the end-products of evolution in their particular lines. It is, then, natural and proper to assume that there have taken place two distinct lines of development from the ancestral type of the Hymenoptera. In the one, the specialization consisted in the suppression of the development of larvapods, as in the Pamphiliidae, and in the other in the suppression of the development of subanal appendages, as in the Xyelidae. These two families, then, represent two independent lines of evolution and are the most generalized families not only of the Tenthredinoidea but of the Hymenoptera. Whether the Xyelidae is more generalized than the Pamphiliidae, or vice versa, must, from the very nature of the case, remain a question till the advancement of our knowledge shall perhaps make the answer possible. There are, however, a few things that should be pointed out regarding this question. If the suppression of the development of larvapods is considered of equal phylogenetic significance with the suppression of the development of the subanal appendages, and if the head and the appendages of these two families alone are compared, there is no doubt that the Pamphiliidae are more generalized than the Xyelidae. But since the subanal appendages are true abdominal appendages homo-



dynamous with the larvapods, and since it is natural to believe that the process of reduction has taken place very slowly by gradual suppression of the appendages, it is not unreasonable to assume that the apodous condition found in the Pamphiliidae represents a much later stage of specialization than the condition of the polypodous larvae of the Xyelidae. The biology of the Pamphiliidae also indicates that this family is perhaps more specialized than the Xyelidae. However, these considerations counterbalance each other, and, when all is said, it is difficult to decide between the two families as to their relative degrees of specialization. This somewhat drawn-out discussion leads to the following conclusions: (1) the progenitor of the Hymenoptera possessed a pair of larvapods on each of the first ten abdominal segments and a pair of segmented subanal appendages on the eleventh segment; (2) the progenitor gave rise to distinct stocks which resulted in the production of larvae with larvapods in one case and with subanal appendages in the other; (3) the Xyelidae represents the former line of evolution and the Pamphiliidae the latter; and (4) the question as to whether the Pamphiliidae is more generalized than the Xyelidae or vice versa is by its nature unanswerable. To the above conclusions it may be added that it is only natural and reasonable to consider the Tenthredinidae as representing the further evolution of the primitive stock from which the Xyelidae had evolved, and the Cephidae, Xiphidriidae, Siricidae, and Oryssidae, in turn, as evolving from the original stock which gave rise to the Pamphiliidae.

The subanal appendages are present only in the Pamphiliidae and Cephidae. In the former they are rather long, setiform, well developed, distinctly three-segmented; in the latter they are minute, vestigial, often fleshy, papilla-like, and indistinctly segmented. Since the embryonic history of these appendages has not been studied, their true nature is not known. There is little doubt but that they are true appendages. If they represent the appendages of the ultimate segment, as has been suggested by certain writers, and correspond to the so-called style of generalized insects, then their presence is an indication of a primitive condition. There is hardly any question as to the common origin of the subanal appendages in the Pamphiliidae and Cephidae, and if these structures represent what they are assumed to represent these two families must have a close affinity.

The ocellaræ are present in the Pamphiliidae, Xyelidae, Tenthredinidae, and Cephidae. They are well developed, and are usually accompanied by well-defined ocularia in the first three families. In the Cephidae the ocellaræ are vestigial and represented by localized pigmented granules, and lack ocularia. It is significant that the ocellaræ are unmodified in the gall-makers and leaf-miners of the family Tenthredinidae, except in *Phlebotrophia*, where they are reduced in size and the ocularia indistinct. The atrophy of the ocellaræ is undoubtedly correlated with the mining habit of the larvae.

The antennae are present in all larvae of the Tenthredinoidea. Judging from the condition obtaining in generalized insects, it is reasonable to consider the antennae of the Pamphiliidae as representing the primitive ancestral type. They are long and setiform in this family and consist of seven cylindrical well-chitinized segments. The Xyelidae is closely related to the preceding family in antennal characters altho a shortening of the length has taken place. In the Tenthredinidae the antennae undergo much modification both in the number and form of the segments. They may be conical, limpet-shaped, or flattened, and the number of segments varies from five to one. The antennae of the Cephidae resemble those of the Xyelidae and some of the Tenthredinidae in shape and number of segments. The antennae undergo steady reduction in size and number of segments in the three remaining families, reaching the extreme of reduction in the Oryssidae, where each is represented by a button-like swelling. The trend of specialization in the antennae is orthogenetic so far as the families are concerned but quite diverse in the subfamilies of the Tenthredinidae.

The mouth-parts, which include the mandibles, maxillae and labium, afford a fertile field for characters which are of interest from a systematic point of view. The mandibles, like the antennae, are the most persistent and ever-present structures in the head of all larvae of the Tenthredinoidea. The maxillary and labial palpi are typically four- and three-segmented respectively. The change is in the reduction in number and size of the segments. The Cephidae is normal in this respect but gradual change takes place in the Xiphydriidae and Siricidae, while in the Oryssidae the change has proceeded so far as to completely obliterate the maxillary and labial palpi. The palpi of Phlebotrophia resemble those of the specialized families. The families represent different stages of specialization, and their relative systematic position can be indicated by the degree of changes in the mouth-parts.

The suranal process which is located on the meson of the suranal lobe or the tenth urotergum is characteristic of the larvae of the Cephidae, Xiphydriidae, and Siricidae. It should not be confused with the caudal protuberances of certain Tenthredinidae, as these two structures are of an entirely different nature. There is a minute hook-like process on the caudo-meson of the tenth abdominal tergum of the Pamphiliidae. It should be noted that in certain larvae of *Pontania* and *Caulocampus* the caudal portion of the ultimate tergum is produced caudad as a blunt more or less strongly chitinized protuberance which undoubtedly serves the same function as the suranal process of the specialized families. These two structural modifications of the caudal end of the body, however, are not homologous with each other. The suranal process is undoubtedly

an adaptive structure which has arisen in response to the habit of the larvae and does not represent the true appendages of the segment, to which the suranal lobe belongs. For this reason the caudal process is of less significance phylogenetically than the subanal appendages of the Pamphiliidae and Cephidae.

The metathoracic spiracles of the larvae are either obsolete or vestigial in the majority of the Tenthredinoidea. The larvae of the Cephidae and Siricidae differ from all others in that the metaspiracles are functional and as large as the abdominal spiracles. It is important to ascertain the original condition of the metaspiracles in these families because upon the interpretation of their primitive condition depends their phylogenetic value and hence the relationship between these two families and also between them and other families. It is considered reasonable to assume that the progenitor of insects and hence the ancestor of the Hymenoptera possessed functional spiracles on all the segments of the body including the metathorax, and that their metaspiracles must have been as large as the abdominal spiracles. The closed minute functionless metaspiracles found in the Pamphiliidae, Xyelidae, and others, indicate a condition of atrophy rather than a rudimentary condition, and so far as this character is concerned the Cephidae and Siricidae represent the unmodified primitive condition and some sort of relation between these two families must be assumed. But on the basis of other characters it is not conceivable that these two families evolved one from the other in a linear sequence, apart from and independent of other families; they must have descended from a common stock which also gave rise to other families which exhibit vestigial metaspiracles. If this is true there must have taken place a series of dichotomies starting with functional metaspiracles, one line of development resulting in the loss of this primitive character and the other line of evolution retaining the original condition. By assuming four such successive dichotomies in the line of evolution, the origin and significance of the metaspiracles of the Cephidae and Siricidae can be reasonably explained. At each of the four successive dichotomous divisions which produced respectively the pamphiliid-like progenitor and Xyelidae, Pamphiliidae and the cephid-like progenitor, Cephidae and the xiphydriid-like progenitor, and Xiphydriidae and Siricidae, one line of descent always carried the original character and the other line lost it until this peculiarity was generally sifted out, being retained unmodified only in the Cephidae and Siricidae. In this way the metaspiracles are here considered to be the direct descendant of the primitive structures which remained unmodified thruout the course of evolution of these families. The two families are generalized in this respect indicating a close genetic relation.



The morphological characters discussed are summarized in the following table:

COMPARISON OF VARIOUS STRUCTURES IN THE FAMILIES OF THE TENTHREDINOIDEA

Structure	Pamphiliidae	Cephidae	Xiphodriidae	Siricidae	Oryssidae	Xyelidae	Tenthredinidae
Thoracic legs	5-segmented	Fleshy	Fleshy	Fleshy	Wanting	5-segmented	5-, 4-, 3-segmented
Larvapods	Wanting	Wanting	Wanting	Wanting	Wanting	10 pairs	6-8 pairs
Subanal appendages	Distinct, long	Vestigial	Wanting	Wanting	Wanting	Wanting	Wanting
Ocellaræ	Distinct	Vestigial	Wanting	Wanting	Wanting	Distinct	Distinct
Antennæ	7-segmented	5- and 4-segmented	3-segmented	1-segmented	1-segmented	7- and 6-segmented	5-, 4-, and 1-segmented
Mouth-parts	Typical	Typical	Modified	Modified	Vestigial	Typical	Typical, rarely modified
Suranal process	Wanting	Distinct	Distinct	Distinct	Wanting	Wanting	Wanting
Metathoracic spiracles	Vestigial	Functional	Vestigial	Functional	Vestigial	Vestigial	Vestigial

The Pamphiliidae, with its long seven-segmented antennæ, setiform three-segmented subanal appendages, setiform five-segmented thoracic legs, well-developed typical mouth-parts, together with the absence of larvapods, is unquestionably one of the most generalized families of the Tenthredinoidea. This family differs from the hypothetical type only in the absence of larvapods and reduced metaspiracles.

The Xyelidae, with its fairly long seven- and six-segmented antennæ, five-segmented thoracic legs, well-developed typical mouth-parts, together with the presence of ten pairs of larvapods and the absence of subanal appendages, is undoubtedly a very generalized family, quite different from the preceding. The only striking difference from the hypothetical type is the absence of the subanal appendages and functional metaspiracles.

The Tenthredinidae, with its one- to five-segmented antennæ, well-developed thoracic legs, and six to eight pairs of larvapods, together with the absence of the subanal appendages, is unquestionably related to the Xyelidae, and if it has not been evolved directly from the latter the two families must have arisen from a common stock. The Tenthredinidae is a phylogenetic complex in itself, and some of the more specialized genera are further removed from the more generalized genera, biologically as well as morphologically, than the latter are from the Xyelidae or their xyelid-like ancestors.

The Cephidae, with its segmented antennæ, vestigial subanal appendages, vestigial thoracic legs, normal mouth-parts, absence of larvapods, presence of suranal process, vestigial ocellaræ, and large functional metaspiracles, is considered an offshoot of the ancestral stem from which



the Pamphiliidae had previously evolved. The specialization is indicated by the vestigial condition of the ocellaræ, subanal appendages, and thoracic legs, on the one hand, and the development of suranal processes on the other. The presence of the functional metaspiracles is of phylogenetic importance. So far as the head characters are concerned, this family resembles the Tenthredinidae to a limited extent, and in some of the generalized genera of the latter the thoracic legs and the caudal portion of the tenth abdominal segment undergo some modifications which in a remote sense simulate the condition in the Cephidae. But since this family differs from the Tenthredinidae, and resembles the Pamphiliidae in the absence of larvapods and the presence of subanal appendages, it is considered more reasonable to ascribe to it a closer relationship to the Pamphiliidae than to the Tenthredinidae.

The Xiphydriidae, with its somewhat modified mouth-parts, three-segmented antennae, fleshly thoracic legs, suranal process, absence of larvapods, the general shape of the body, and its biology, resembles the Cephidae but differs from it in the absence of subanal appendages, ocellaræ, and in the vestigial functionless metaspiracles. The absence of the subanal appendages may point to one of the two possibilities in regard to the origin of the Xiphydriidae. This family might have evolved from the cephid-like ancestor but have lost the subanal appendages by the completion of the process of atrophy which had already reduced the original distinctly-segmented appendages (similar to those of the Pamphiliidae) to the vestigial papilliform appendages of the Cephidae. The two families under consideration might, on the other hand, have had a common stem which possessed subanal appendages, ocellaræ, and vestigial metaspiracles. In the absence of positive support for the first possibility, it is more expedient to consider the second possibility as nearer to the true relationship of the two families, Xiphydriidae and Cephidae.

The Siricidae, with its greatly reduced thoracic legs and mouth-parts together with certain other characters, is considered more specialized than the Xiphydriidae. The presence of the functional metaspiracles and its genetic significance have already been discussed. For the same reason which suggests a common origin for the Cephidae and Xiphydriidae, the Siricidae is considered to have arisen from a common stock which gave rise also to the Xiphydriidae. In the degree of specialization by reduction as well as by addition, this family outranks the Xiphydriidae.

The Oryssidae, with its vestigial mouth-parts, absence of ocellaræ, thoracic and abdominal legs, subanal appendages, suranal process, caudal protuberances, and functional metaspiracles, together with its parasitic habit, is unquestionably the most highly specialized family of the Tenthredinoidea. Its morphological and biological characters are so different from other families that it is not easy to ascertain the systematic position

of the family. There are, however, certain considerations which suggest a possible relationship between this family and the Siricidae. Morphologically the oryssid larvae are more closely related to the apodous boring larvae of the Cephidae, Xiphydriidae, and Siricidae than to the polypodous free-living larvae of the Xyelidae and Tenthredinidae. The siricid larvae are more closely related to those of the Oryssidae than to those of the Cephidae and Xiphydriidae. The parasitic habit also suggests a closer relation to the wood-boring larvae since it is more plausible to imagine the possibility of a wood-boring larvae becoming parasitic on other wood-boring insect larvae under some unknown but not entirely inconceivable circumstances than to imagine the development of a parasitic habit *de novo* in free-living leaf-feeders. Since the oryssid larvae are parasitic on the larvae of Buprestis inhabiting plants which are also infested by the larvae of the Siricidae, if any transformation of habit of the larvae has taken place, it is more natural to expect the larvae of the Siricidae or some siricid-like insect to become parasitic than any other larvae. The recent investigation by Baumberger (1919) on the rôle of microorganisms in the physiology of insect nutrition offers a valuable suggestion in regard to the possibility of radical changes in food habits. For these reasons it is considered reasonable to ascribe a common progenitor to the Siricidae and Oryssidae, at least for the time being. It may be added that it is not entirely unreasonable to assume an independent line of evolution for the Oryssidae apart from all other Tenthredinoidea and consider this family as having no close relation to any of the modern families of the Tenthredinoidea. In that case, the Oryssidae must have arisen from the ancestral stock before the Pamphiliidae and Xyelidae had their origin. There is, however, no clear evidence in support of such relation and since the relation is reasonably explained by associating the Oryssidae with the Siricidae, the former is considered the most highly specialized family of the Tenthredinoidea with a common origin with the ancestor of the Siricidae.

The conclusions on the systematic position and relationship of the different families of the Tenthredinoidea based exclusively on larval characters and derived entirely independent of the opinions of the specialists who have paid more attention to the adults are of necessity not the final words on the subject. The true significance of such conclusions lies in their complemental and collateral value. It is interesting on this account to compare the writer's opinion with the conclusions of the modern authorities on this group of the Hymenoptera.

The relationship suggested here supports in its essential points the three more important systems of classification proposed by Konow (1905), MacGillivray (1906), and Rohwer (1911). MacGillivray considered the Xyelidae the most primitive because of the venational character but

recognized the Pamphiliidae as the most generalized from his study (1913) of the immature stages. Had he placed the Pamphiliidae before the Xyelidae and the Cephidae before the Xiphydriidae and Siricidae, his system would coincide exactly with the system based exclusively on the immature stages. Konow and Rohwer both associate the Cephidae with the Pamphiliidae and Xyelidae. This arrangement is partly supported if the affinity between the Pamphiliidae and Cephidae, as suggested in this study, is upheld. The genetic continuity of the Xyelidae and Tenthredinidae is clearly recognized by MacGillivray (1913). The true systematic position of the Tenthredinidae or its equivalent is difficult to express in linear arrangement. The important point to be noted is the fact that these authors and also Morice (1919) consider the Xyelidae and Tenthredinidae as different and apart from the other families of the Tenthredinoidea. The Oryssidae unquestionably merits at least separate family rank. In the absence of requisite knowledge of the larval characters of the Hymenoptera other than the Tenthredinoidea, it is not expedient to venture any opinion on the suggestion made by Rohwer and Cushman (1917) to establish a third suborder, Idiogastra, for the reception of the Oryssidae. Enslin (1911) differs from the authors already mentioned not only in his arrangement of the groups in a descending order but also in treating the Xyelidae and Pamphiliidae as subfamilies of his Tenthredinidae, on a level with the Cimbicini, Lophrini, and others. This study does not support his arrangement. Morice (1919) suggested that "the Lydini (Pamphiliidae Ensl.) may represent a primitive group of Tenthredinidae which had branched off from the main stock before it had developed certain characters," such as abdominal legs. Handlirsch (1908) considered the Siricidae as having evolved from the osculant Juracic group, Pseudo-siricidae. The antiquity of the Siricidae is accepted by Morice who expresses his idea of the relationship of the families of the Tenthredinoidea as follows: "We may suppose that the Siricidae are the earlier group, but whether the Tenthredinidae and Lydini had Siricid ancestors, or whether the Siricidae+Cephini+Oryssidae and Tenthredinidae+Lydini are respectively earlier and later branches of a common stock are questions which must be left unanswered."



## V. SUMMARY

The larvae of the Tenthredinoidea have proved to be of great value in affording important evidence in regard to the probable phylogenetic relationship of the families included in this superfamily. The more significant conclusions reached in this study are summarized in the form of a synoptic key as follows:

## FAMILIES OF TENTHREDINOIDEA

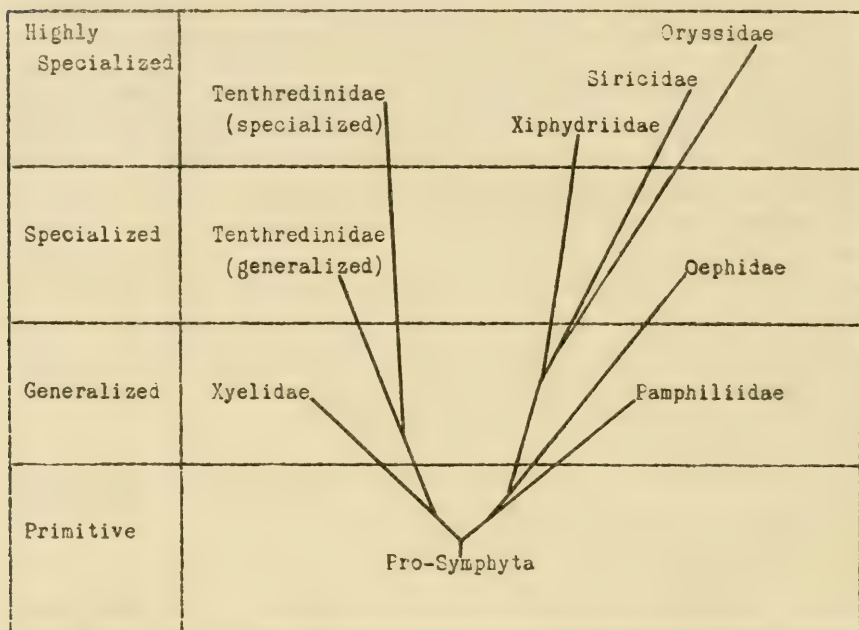
- Larvopods present, thoracic legs present, well developed, distinctly segmented.
  - Larvopods present on all abdominal segments.....*Xyelidae*
  - Larvopods never present on 1st and 9th abdominal segments.....*Tenthredinidae*
- Larvopods wanting, thoracic legs present or wanting.
  - Thoracic legs present.
    - Thoracic legs and subanal appendages well-developed and distinctly segmented.  
*Pamphiliidae.*
    - Thoracic legs vestigial, indistinctly segmented.
      - Subanal appendages and ocellaræ present.....*Cephidae.*
      - Subanal appendages and ocellaræ wanting.
        - Metaspiracles vestigial, much smaller than abdominal spiracles...*Xiphydriidae.*
        - Metaspiracles functional, as large as abdominal spiracles.....*Siricidae.*
    - Thoracic legs wanting.....*Oryssidae.*

A synopsis such as the foregoing is necessarily inadequate and somewhat misleading in indicating the affinities of the families. A better idea is gained by means of the customary phylogenetic tree, altho such a scheme also has its limitations. In the following diagram the relation between the families of the Tenthredinoidea is shown. Here the relative vertical positions are intended to represent approximately the degree of specialization; and the continuous lines, the affinities.

The larvae of the Tenthredinoidea are thus divisible into two distinct groups. The first group includes the larvae characterized by the presence of both the thoracic and abdominal legs, and by the absence of the subanal appendages and suranal process, and is represented by the *Xyelidae* and *Tenthredinidae*. The second group consists of the five families, *Pamphiliidae*, *Cephidae*, *Xiphydriidae*, *Siricidae*, and *Oryssidae*, and is divisible into two subgroups. The first subgroup contains the first four families and is characterized by the absence of abdominal legs, by the



presence of vestigial clawless thoracic legs in the last three families, and by the presence of either subanal appendages or suranal process or both. The second subgroup contains a single family, Oryssidae, which is characterized by the absence of both thoracic and abdominal legs, suranal



Phylogenetic tree indicating the probable affinities of various families of the Tenthredinoidea

process, subanal appendages, and segmented maxillary and labial palpi. The Xyelidae and Pamphiliidae are undoubtedly the most primitive of the first and second groups respectively.

The Tenthredinoidea, therefore, is considered to have developed from a common ancestral stock along two distinct lines of evolution. The first line of development led to the evolution of the Xyelidae and Tenthredinidae and the second line produced the Pamphiliidae, Cephidae, Xiphydriidae, Siricidae, and Oryssidae.

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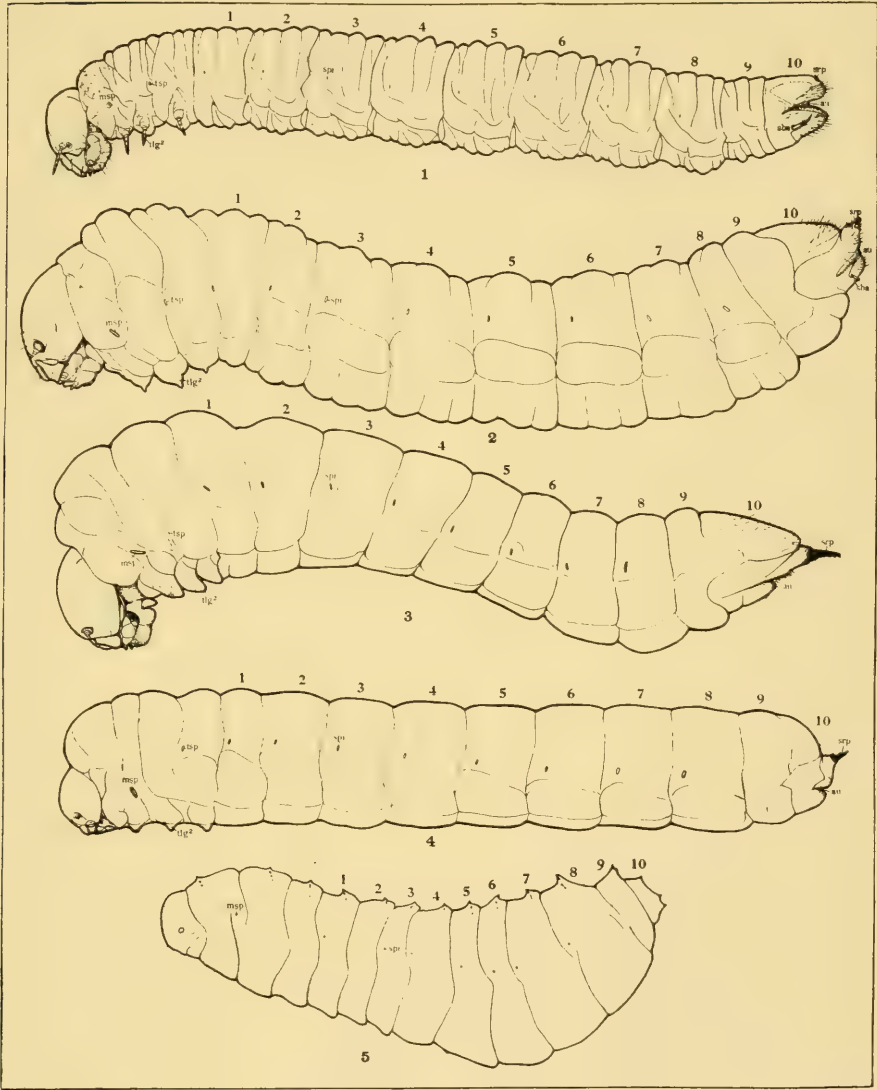
## PLATE I



EXPLANATION OF PLATE  
LARVAE OF TENTHREDINOIDEA

- Fig. 1—Pamphiliidae. *Pamphilius* sp. Y-125.  
Fig. 2—Cephidae. *Janus integer*.  
Fig. 3—Xiphydriidae. *Xiphydria* sp.  
Fig. 4—Siricidae. *Tremex columba*.  
Fig. 5—Oryssidae. *Oryssus occidentalis*  
(After Rohwer and Cushman, 1917).

*au*    anus  
*msp*   mesothoracic spiracle  
*sba*   subanal appendage  
*spi*   abdominal spiracle  
*srp*   suranal process  
*ulg<sup>2</sup>*   mesothoracic leg  
*lsp*   metathoracic spiracle





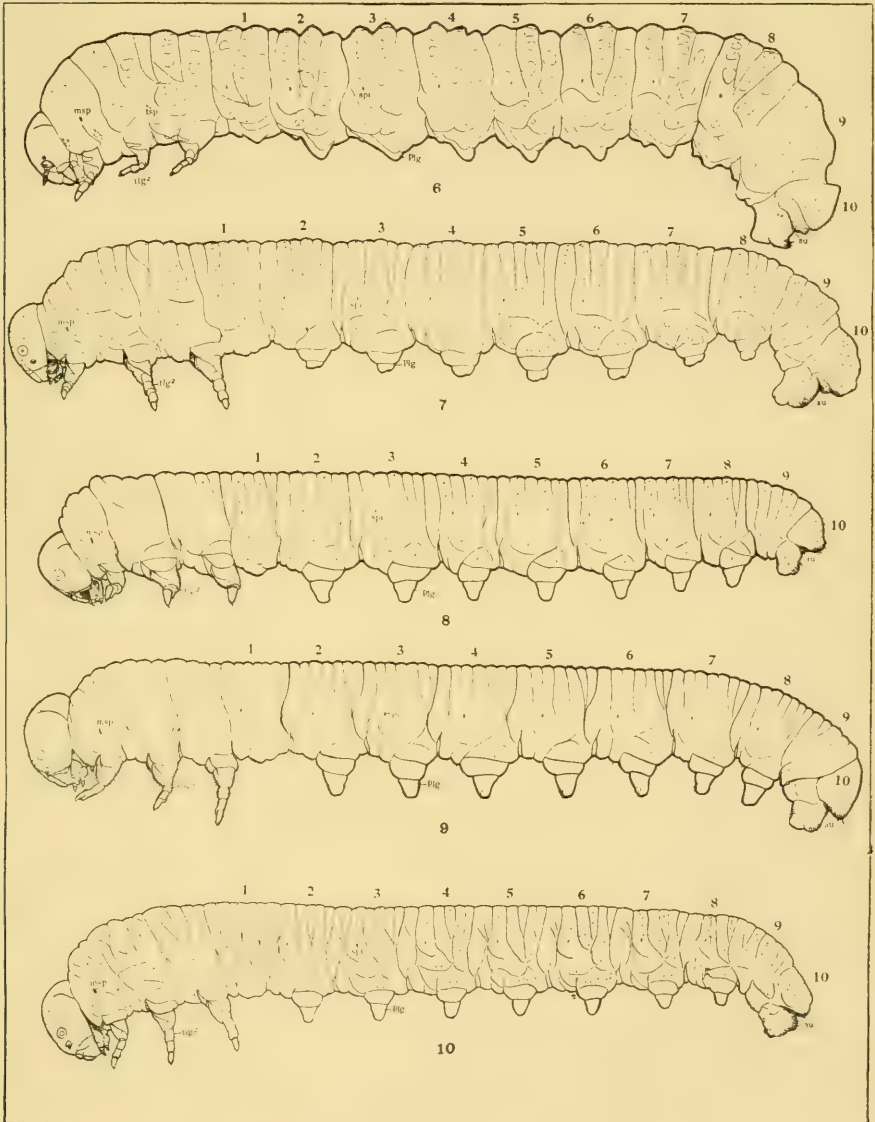
## PLATE II



## EXPLANATION OF PLATE

## LARVAE OF XYELIDAE AND TENTHREDINIDAE

- Fig. 6—Xyelidae. *Megaxyela major*.  
 Fig. 7—Tenthredinidae. Diprioninae. *Neodiprion lecontei*.  
 Fig. 8—Tenthredinidae. Emphytinae. *Emphytus apertus*.  
 Fig. 9—Tenthredinidae. Selandriinae. *Strongylogaster annulosus*.  
 Fig. 10—Tenthredinidae. Dolerinae. *Dolerus similis*.
- au* anus  
*m<sup>sp</sup>* mesothoracic spiracle  
*plg* larvaped  
*spi* abdominal spiracle  
*lg<sup>2</sup>* mesothoracic leg  
*tsp* metathoracic spiracle





## PLATE III

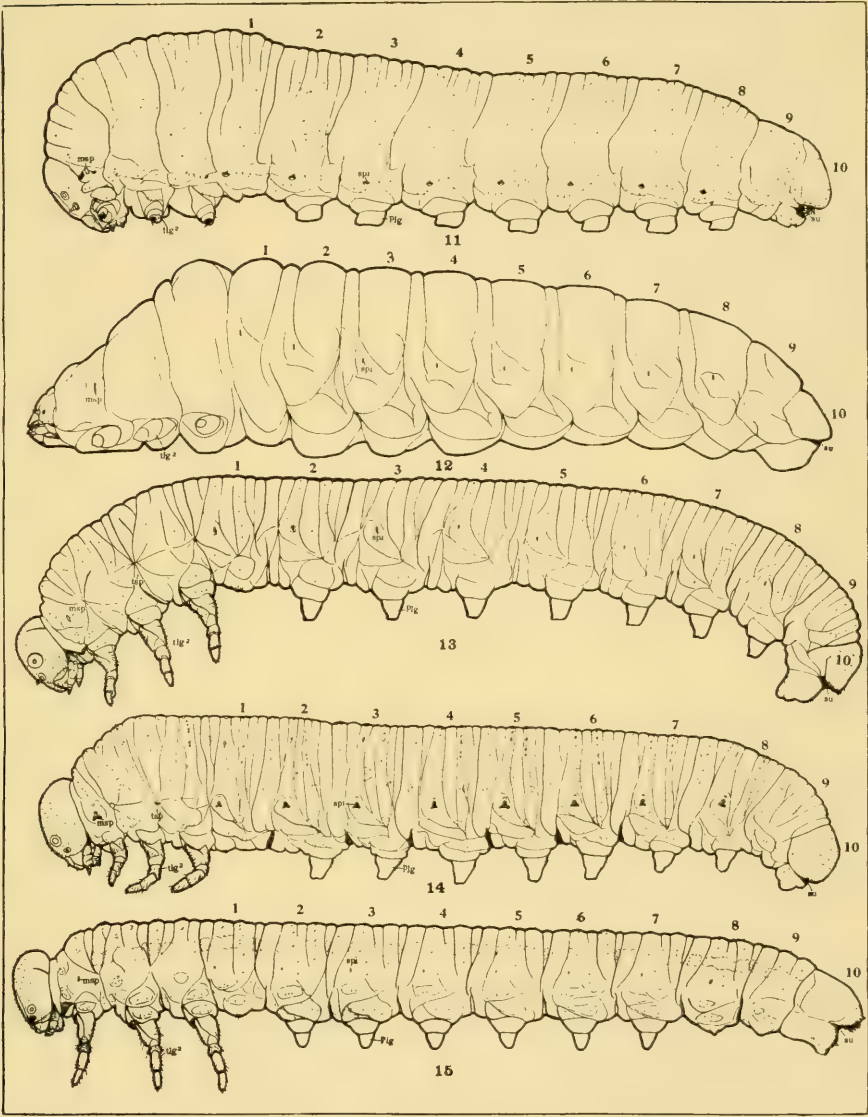


## EXPLANATION OF PLATE

## LARVAE OF TENTHREDINIDAE

- Fig. 11—Phyllotominae. *Caliroa cerasi*.  
Fig. 12—Phyllotominae. *Phlebatrophia mathesoni*.  
Fig. 13—Tenthredininae. *Tenthredo* sp.  
Fig. 14—Cimbicinae. *Abia inflata*.  
Fig. 15—Hoplocampinae. *Hemichroa americana*.

*an* anus  
*msp* mesothoracic spiracle  
*plg* larvopod  
*spi* abdominal spiracle  
*lg<sup>2</sup>* mesothoracic leg  
*tsp* metathoracic spiracle





## PLATE IV

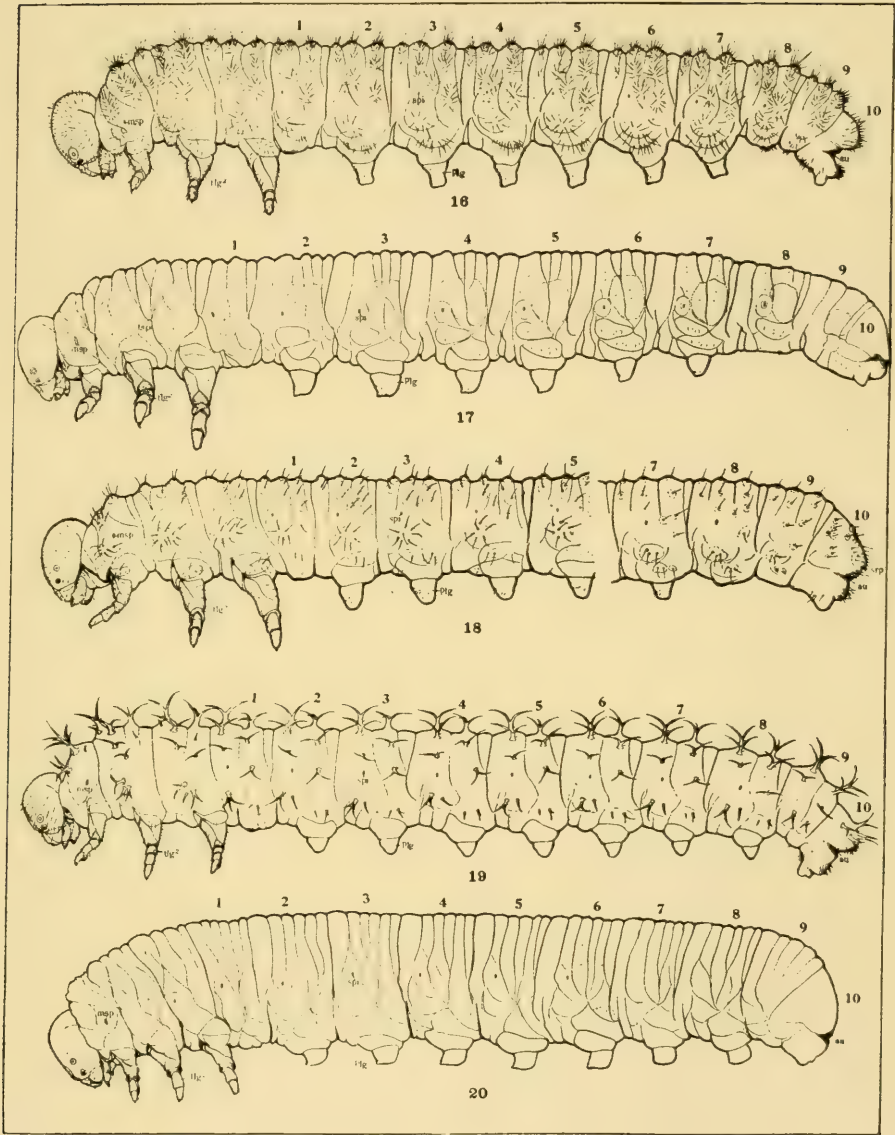


## EXPLANATION OF PLATE

## LARVAE OF TENTHREDINIDAE

- Fig. 16—Cladiinae. *Cladius pectinicornis*.  
Fig. 17—Nematinae. *Pteronidea ventralis*.  
Fig. 18—Nematinae. *Pteronidea ribesi*.  
Fig. 19—Blennocampinae. *Monophadnoides rubi*.  
Fig. 20—Blennocampinae. *Tomostethus bardus*.

<i>an</i>	anus
<i>msp</i>	mesothoracic spiracle
<i>plg</i>	larvapod
<i>spi</i>	abdominal spiracle
<i>srp</i>	suranal process
<i>lg<sup>a</sup></i>	mesothoracic leg
<i>tsp</i>	metathoracic spiracle





## PLATE V

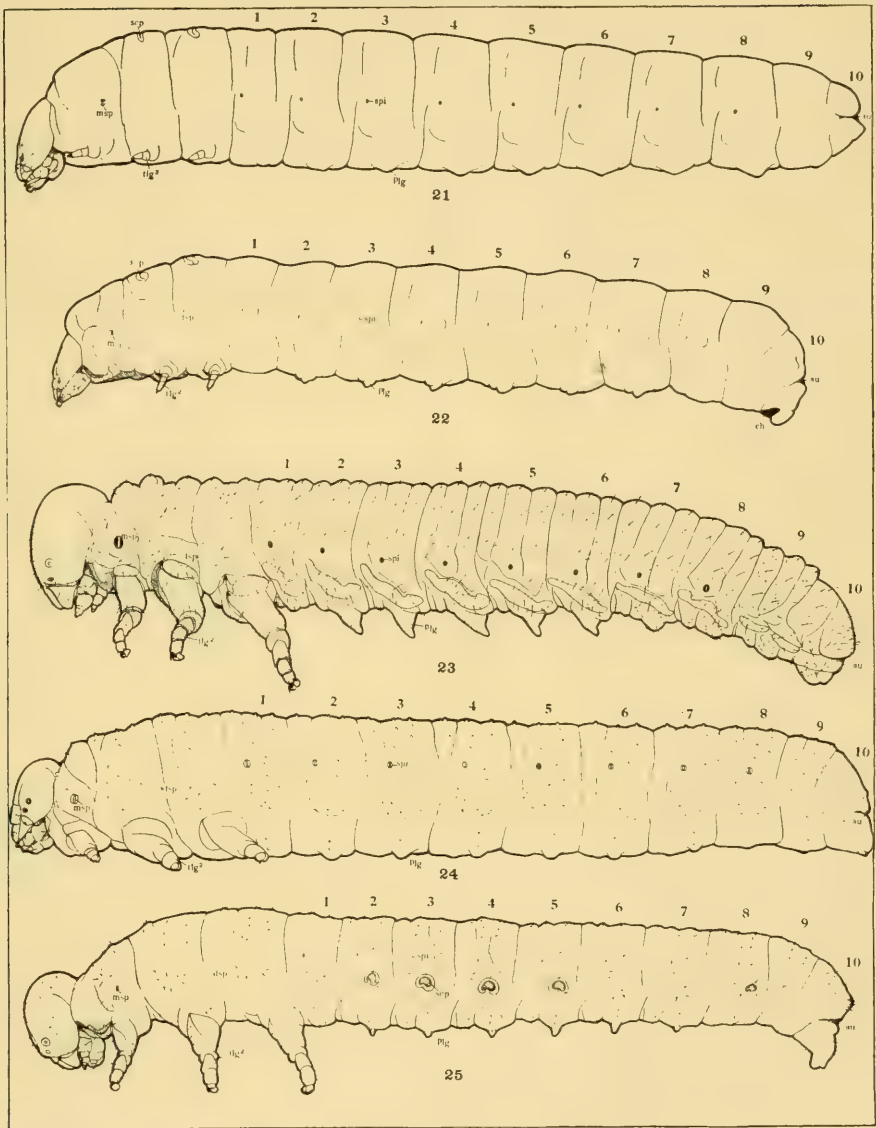


## EXPLANATION OF PLATE

## LARVAE OF TENTHREDINIDAE

- Fig. 21—Fenusinae. *Kaliofenusa ulmi*.  
Fig. 22—Scolioneurinae. *Metallus rubi*.  
Fig. 23—Hylotominae. *Hylotoma* sp.  
Fig. 24—Schizocerinae. *Schizocerus zabriskei*.  
Fig. 25—Acordulecerinae. *Acordulecera* sp.

*au* anus  
*m<sub>sp</sub>* mesothoracic spiracle  
*plg* larvopod  
*sc<sub>p</sub>* sucker-like protuberance  
*spi* abdominal spiracle  
*tlg<sup>2</sup>* mesothoracic leg  
*ts<sub>p</sub>* metathoracic spiracle





## PLATE VI



## EXPLANATION OF PLATE

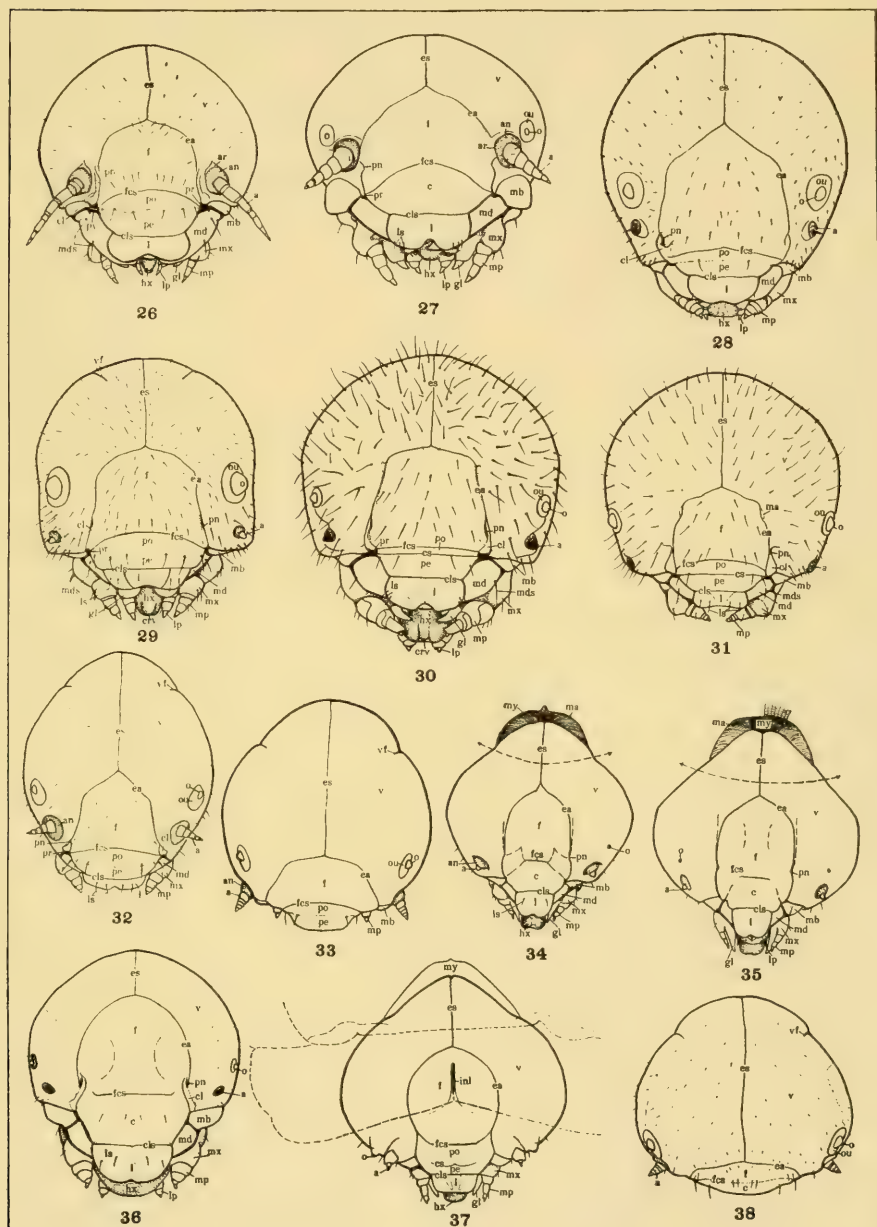
## CEPHALIC ASPECT OF THE HEAD

Fig. 26—*Pamphilius* sp.  
 Fig. 27—*Megaxyela major*.  
 Fig. 28—*Neodiprion lecontei*.  
 Fig. 29—*Abia americana*.  
 Fig. 30—*Pteronidea ribesi*.  
 Fig. 31—*Lygaeonematus erichsoni*.  
 Fig. 32—*Endelomyia aethiops*.

Fig. 33—*Macremphytus variamus*.  
 Fig. 34—*Kaliofenusa ulmi*.  
 Fig. 35—*Metallus rubi*.  
 Fig. 36—*Schizocerus zabriskei*.  
 Fig. 37—*Phlebotrophia mathesoni*.  
 Fig. 38—*Dolerus similis*.

*a* antenna  
*an* antacoria  
*ar* antennaria  
*c* clypeus  
*cl* clypealia  
*cls* clypeo-labral suture  
*crv* sericos  
*cs* clypeal suture  
*ea* epicranial arm  
*es* epicranial stem  
*f* front  
*fcs* fronto-clypeal suture  
*gl* galea  
*hx* hypopharynx  
*inl* line of invagination  
*l* labrum  
*lp* labial palpus  
*ls* labral setae

*ma* muscular attachment  
*mb* mandibularia  
*md* mandible  
*mds* mandibular setae  
*mp* maxillary palpus  
*mx* maxilla  
*o* ocellara  
*ou* ocellaria  
*pe* preclypeus  
*pn* pretentorina  
*po* postclypeus  
*pr* precoila  
*py* preartis  
*v* vertex  
*vf* vertical furrow





## PLATE VII



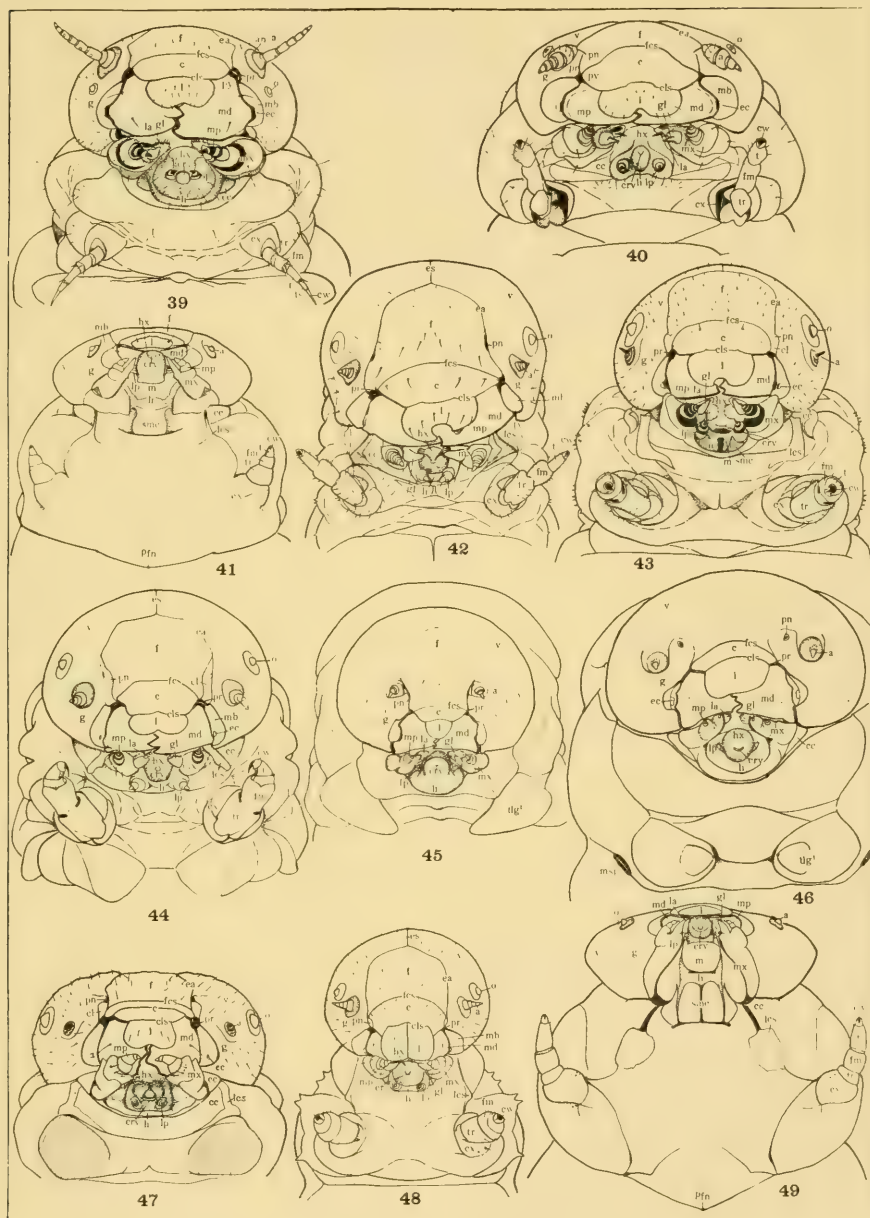
## EXPLANATION OF PLATE

## VENTRAL ASPECT OF THE HEAD AND PROTHORAX

Fig. 39—*Pamphilus* sp.Fig. 40—*Megaxyela major*.Fig. 41—*Kaliofenusa ulmi*.Fig. 42—*Dolerus similis*.Fig. 43—*Neodiprion lecontei*.Fig. 44—*Macremphytus varianus*.Fig. 45—*Xiphydria* sp.Fig. 46—*Tremex columba*.Fig. 47—*Lygeonematus erichsoni*.Fig. 48—*Endelomyia aethiops*.Fig. 49—*Metallus rubi*.

*a* antenna  
*an* antacoria  
*c* clypeus  
*cc* cervacoria  
*cl* clypealia  
*cls* clypeo-labral suture  
*crv* sericos  
*cw* tarsal claw  
*cx* coxa  
*ea* epicranial arm  
*ec* extensacuta  
*es* epicranial stem  
*f* front  
*fcs* fronto-clypeal suture  
*fm* femur  
*g* gena  
*gl* galea  
*hx* hypopharynx

*l* labrum  
*la* lacinia  
*lcs* lateral cervical sclerite  
*li* labium  
*lp* labial palpus  
*mb* mandibularia  
*md* mandible  
*mp* maxillary palpus  
*mx* maxilla  
*o* ocellara  
*psn* profurcellina  
*pn* pretentorina  
*pr* precoila  
*py* preartitis  
*t* tibia  
*tr* trochanter  
*ug<sup>1</sup>* prothoracic leg  
*v* vertex





## PLATE VIII



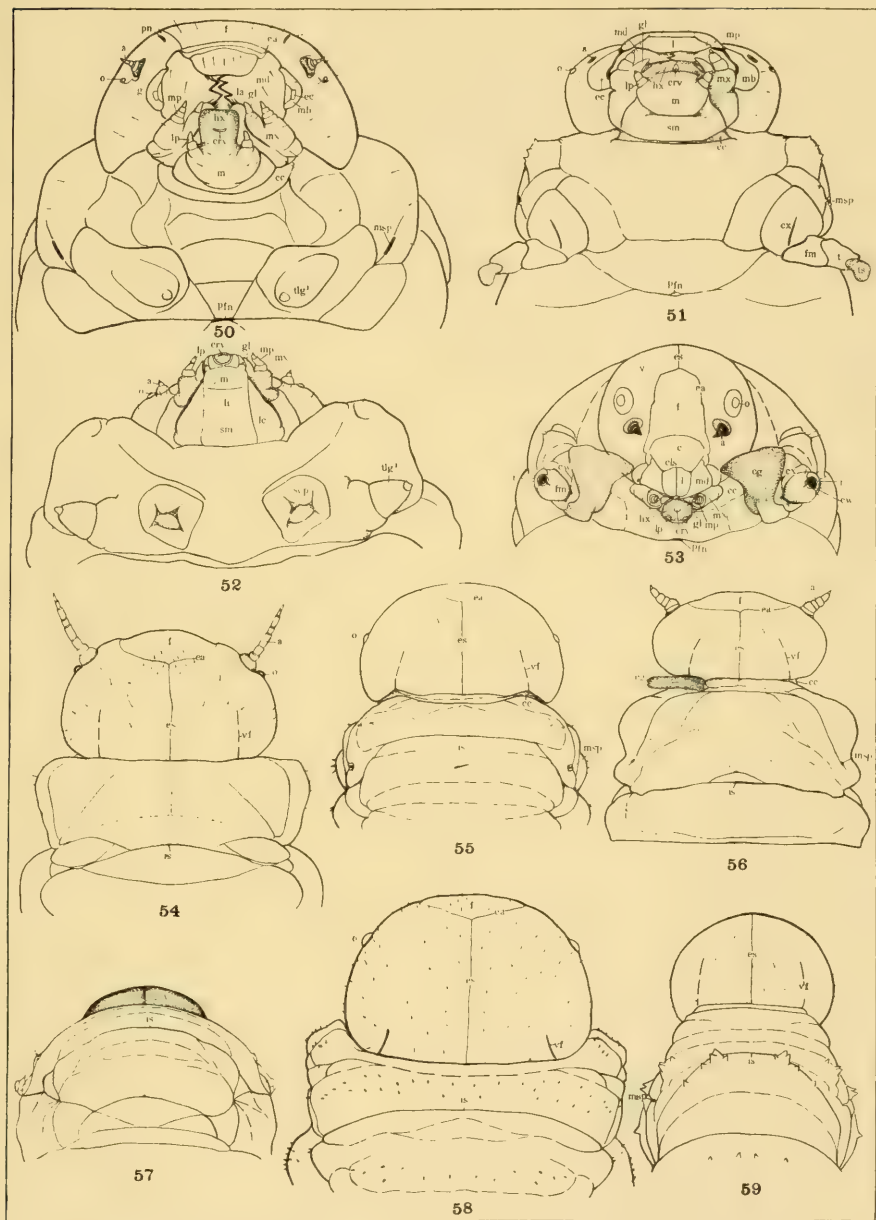
## EXPLANATION OF PLATE

## VENTRAL AND DORSAL ASPECTS OF HEAD AND PROTHORAX

Fig. 50—*Janus integer*.Fig. 51—*Schizocerus zabriskei*.Fig. 52—*Phlebotrophia mathesoni*.Fig. 53—*Caliroa cerasi*.Fig. 54—*Pamphilus* sp.Fig. 55—*Dolerus similis*.Fig. 56—*Megaxyela major*.Fig. 57—*Caliroa cerasi*.Fig. 58—*Neodiprion lecontei*.Fig. 59—*Endelomyia aethiops*.

<i>a</i>	antenna
<i>c</i>	clypeus
<i>cc</i>	cervacoria
<i>cg</i>	cervical gland
<i>cls</i>	clypeo-labral suture
<i>crv</i>	sericos
<i>cw</i>	tarsal claw
<i>cx</i>	coxa
<i>ea</i>	epicranial arm
<i>ec</i>	extensacuta
<i>es</i>	epicranial stem
<i>f</i>	front
<i>fm</i>	femur
<i>g</i>	gena
<i>gl</i>	galea
<i>hx</i>	hypopharynx
<i>is</i>	intersegmental line (limit of somite)
<i>l</i>	labrum

<i>la</i>	lacinia
<i>lc</i>	labicoria
<i>li</i>	labium
<i>lp</i>	labial palpus
<i>m</i>	mentum
<i>mb</i>	mandibularia
<i>md</i>	mandible
<i>mp</i>	maxillary palpus
<i>msp</i>	mesothoracic spiracle
<i>mx</i>	maxilla
<i>o</i>	ocellara
<i>pf<sub>n</sub></i>	profurcellina
<i>pn</i>	pretentorina
<i>t</i>	tibia
<i>tg<sup>1</sup></i>	prothoracic leg
<i>ts</i>	tarsus
<i>v</i>	vertex
<i>vf</i>	vertical furrow





## PLATE IX



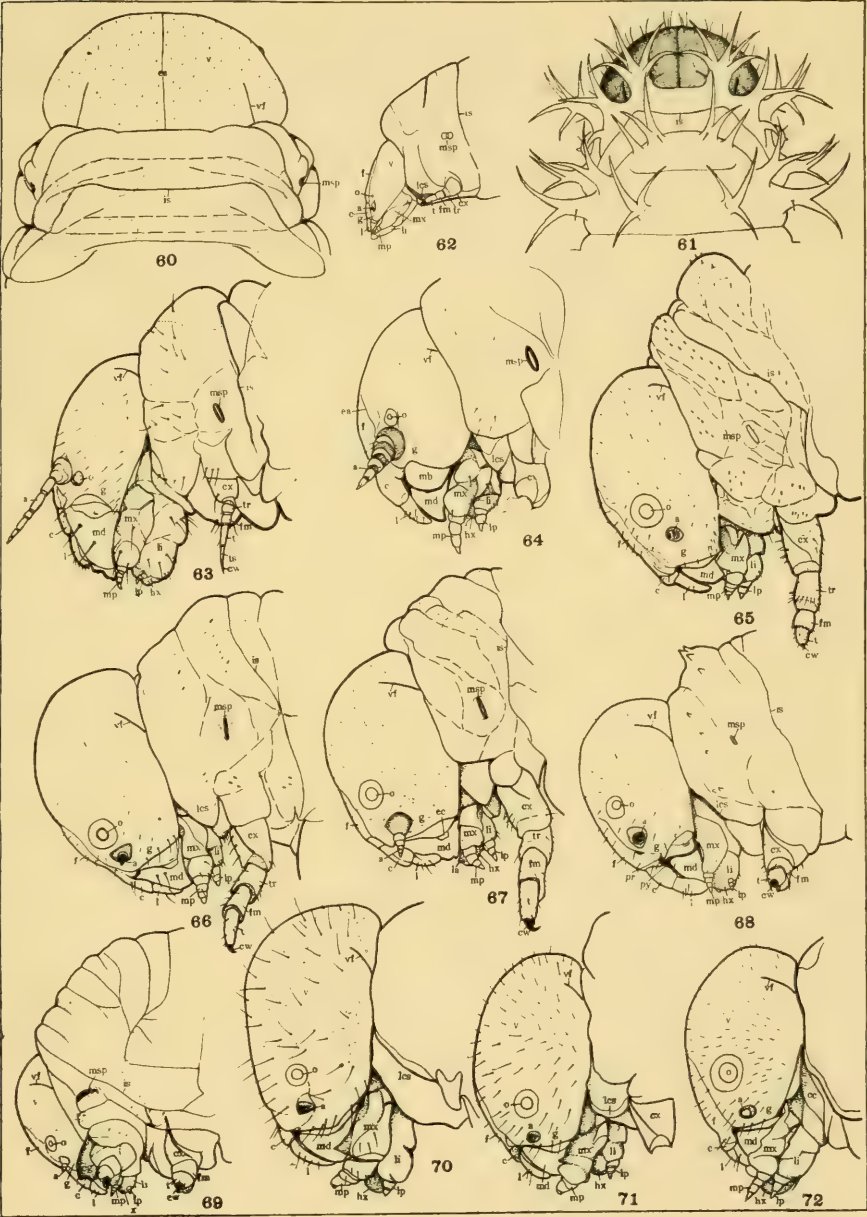
## EXPLANATION OF PLATE

## DORSAL AND LATERAL ASPECTS OF HEAD AND PROTHORAX

Fig. 60—*Macremphytus varians*.Fig. 61—*Monophaednoides rubi*.Fig. 62—*Metallus rubi*.Fig. 63—*Pamphilius* sp.Fig. 64—*Megaxyela major*.Fig. 65—*Neodiprion lecontei*.Fig. 66—*Dolerus similis*.Fig. 67—*Macremphytus varians*.Fig. 68—*Endelomyia aethiops*.Fig. 69—*Caliroa cerasi*.Fig. 70—*Pteronidea ribesi*.Fig. 71—*Lygeonematus erichsoni*.Fig. 72—*Abia americana*.

<i>a</i>	antenna
<i>c</i>	clypeus
<i>cc</i>	cervacoria
<i>cg</i>	cervical gland
<i>cw</i>	tarsal claw
<i>cx</i>	coxa
<i>ea</i>	epicranial arm
<i>ec</i>	extensacuta
<i>es</i>	epicranial stem
<i>f</i>	front
<i>fm</i>	femur
<i>g</i>	gena
<i>hx</i>	hypopharynx
<i>is</i>	intersegmental line (limit of somite)
<i>l</i>	labrum
<i>li</i>	lacinia

<i>lcs</i>	lateral cervical sclerite
<i>li</i>	labium
<i>lp</i>	labial palpus
<i>mb</i>	mandibularia
<i>md</i>	mandible
<i>mp</i>	maxillary palpus
<i>msh</i>	mesothoracic spiracle
<i>mx</i>	maxilla
<i>o</i>	ocellara
<i>pr</i>	precoila
<i>py</i>	preartis
<i>t</i>	tibia
<i>tr</i>	trochanter
<i>v</i>	vertex
<i>vf</i>	vertical furrow





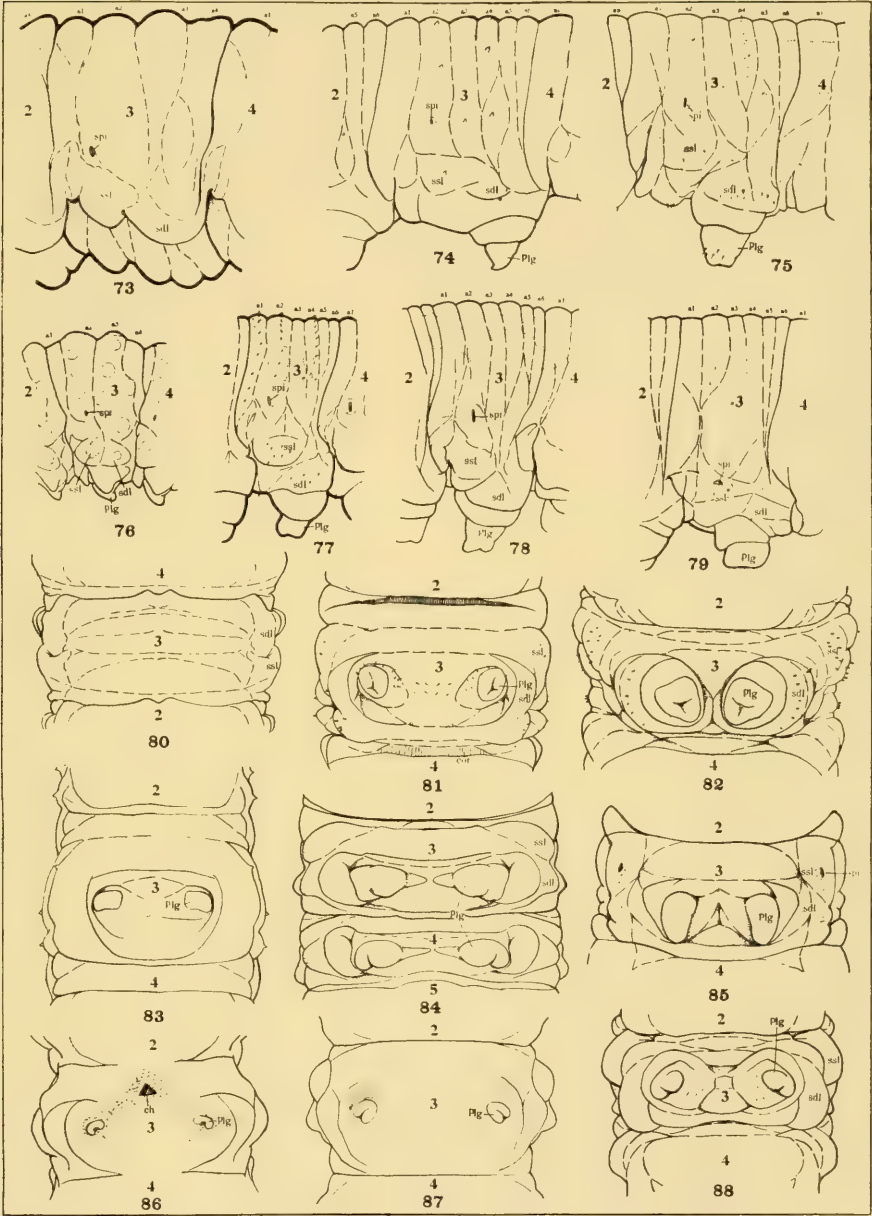
## PLATE X



## EXPLANATION OF PLATE

## LATERAL AND VENTRAL ASPECTS OF THIRD ABDOMINAL SEGMENT

Fig. 73—*Pamphilius* sp.Fig. 74—*Endelomyia aethiops*.Fig. 75—*Dolerus similis*.Fig. 76—*Megaxyela major*.Fig. 77—*Neodiprion lecontei*.Fig. 78—*Macremphytus varianus*.Fig. 79—*Caliroa cerasi*.Fig. 80—*Pamphilius* sp.Fig. 81—*Dolerus similis*.Fig. 82—*Neodiprion lecontei*.Fig. 83—*Endelomyia aethiops*.Fig. 84—*Megaxyela major*.Fig. 85—*Caliroa cerasi*.Fig. 86—*Kaliofenusa ulmi*.Fig. 87—*Metallus rubi*.Fig. 88—*Macremphytus varianus*.*a1-a7* annulets 1, 2, 3, 4, 5, 6, 7.*ch* chitinized area.*cor* intersegmental coria*plg* larvaped*sdl* surpedal lobe or area*spi* abdominal spiracle*ssl* subspiracular lobe or area





## PLATE XI.



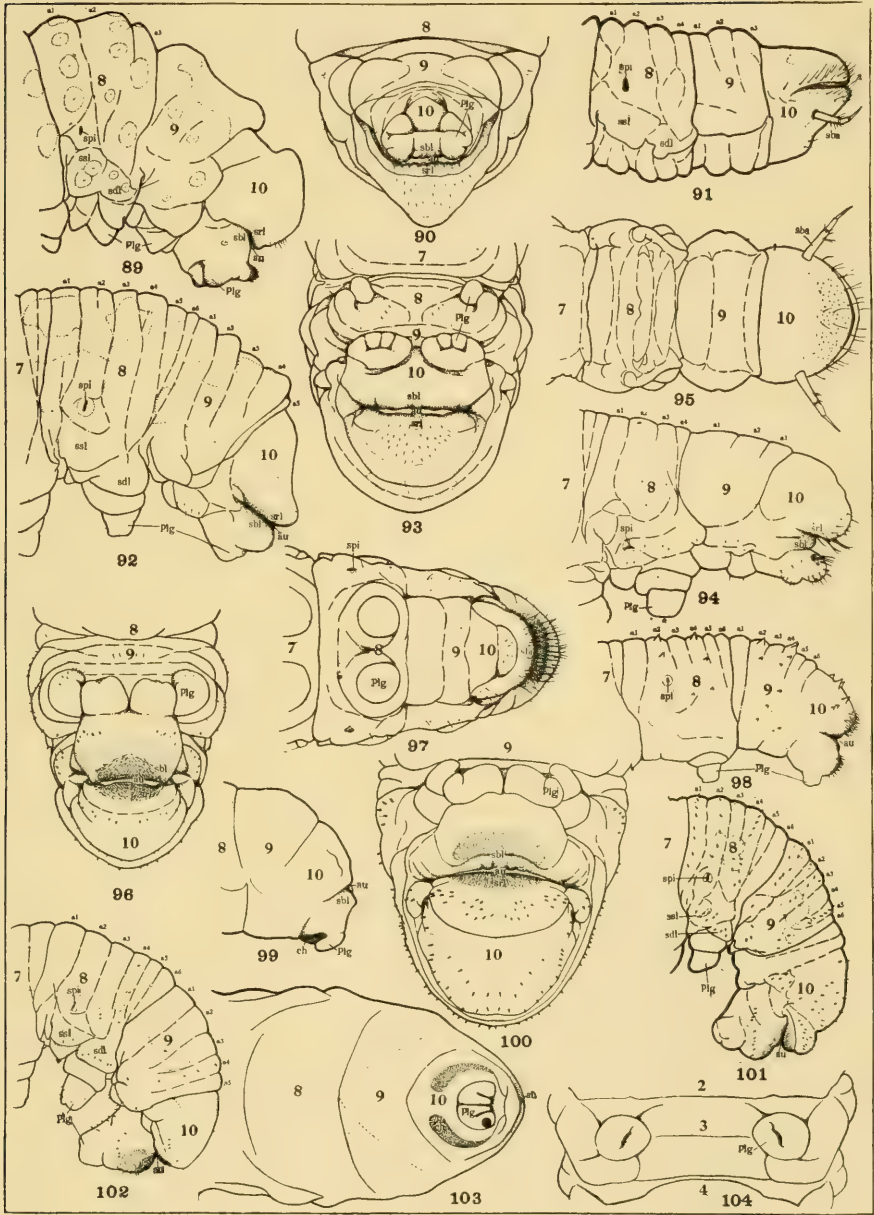
## EXPLANATION OF PLATE

## LATERAL AND VENTRAL ASPECTS OF CAUDAL ABDOMINAL SEGMENTS

Fig. 89—*Megaxyela major*.Fig. 90—*Megaxyela major*.Fig. 91—*Pamphilus* sp.Fig. 92—*Macremphytus varianus*.Fig. 93—*Macremphytus varianus*.Fig. 94—*Caliroa cerasi*.Fig. 95—*Pamphilus* sp.Fig. 96—*Dolerus similis*.Fig. 97—*Caliroa cerasi*.Fig. 98—*Endelomyia aethiops*.Fig. 99—*Metallus rubi*.Fig. 100—*Neodiprion lecontei*.Fig. 101—*Neodiprion lecontei*.Fig. 102—*Dolerus similis*.Fig. 103—*Metallus rubi*.Fig. 104—*Phlebotrophia mathesoni*.

Ventral aspect of third abdominal segment.

<i>au</i>	anus
<i>a1</i>	annulet 1
<i>a2</i>	annulet 2
<i>a6</i>	annulet 6
<i>ch</i>	chitinized area
<i>plg</i>	larvapod
<i>sba</i>	subanal appendage
<i>sbl</i>	subanal lobe
<i>sdl</i>	surpedal lobe or area
<i>spi</i>	abdominal spiracle
<i>srl</i>	suranal lobe
<i>ssl</i>	subspiracular lobe or area





## PLATE XII



## EXPLANATION OF PLATE

## CAUDAL ASPECT OF HEAD, ABDOMEN, ABDOMINAL APPENDAGES

Fig. 105—*Kaliofenusa ulmi*. Ventral aspect of caudal abdominal segment.

Fig. 106—*Phlebotrophia mathesoni*.

Fig. 107—*Xiphydria* sp.

Fig. 108—*Cephus pygmaeus*.

Fig. 109—*Adirus trimaculatus*.

Fig. 110—*Xiphydria* sp.

Fig. 111—*Hartigia cressoni*.

Fig. 112—*Janus integer*.

Fig. 113—*Tremex columba*.

Fig. 114—*Cephus pygmaeus*. Caudal end of the abdomen enlarged.

Fig. 115—*Adirus trimaculatus*.

Fig. 116—*Adirus trimaculatus*. Subanal appendage enlarged.

Fig. 117—*Hartigia cressoni*. Subanal appendage enlarged.

Fig. 118—*Janus* sp. Subanal appendage enlarged.

Fig. 119—*Cephus pygmaeus*. Subanal appendage enlarged.

Fig. 120—*Tremex columba*. Lateral aspect of suranal process enlarged.

Fig. 121—*Janus integer*. Lateral aspect of suranal process enlarged.

Fig. 122—*Tremex columba*. Dorsal aspect of suranal process enlarged.

Fig. 123—*Janus integer*. Dorsal aspect of suranal process enlarged.

Fig. 124—*Pteronidea ribesi*. Ventral aspect of third abdominal segment.

Fig. 125—*Pteronidea ribesi*. Lateral aspect of caudal end of abdomen.

Fig. 126—*Pteronidea ribesi*. Lateral aspect of caudal end of abdomen.

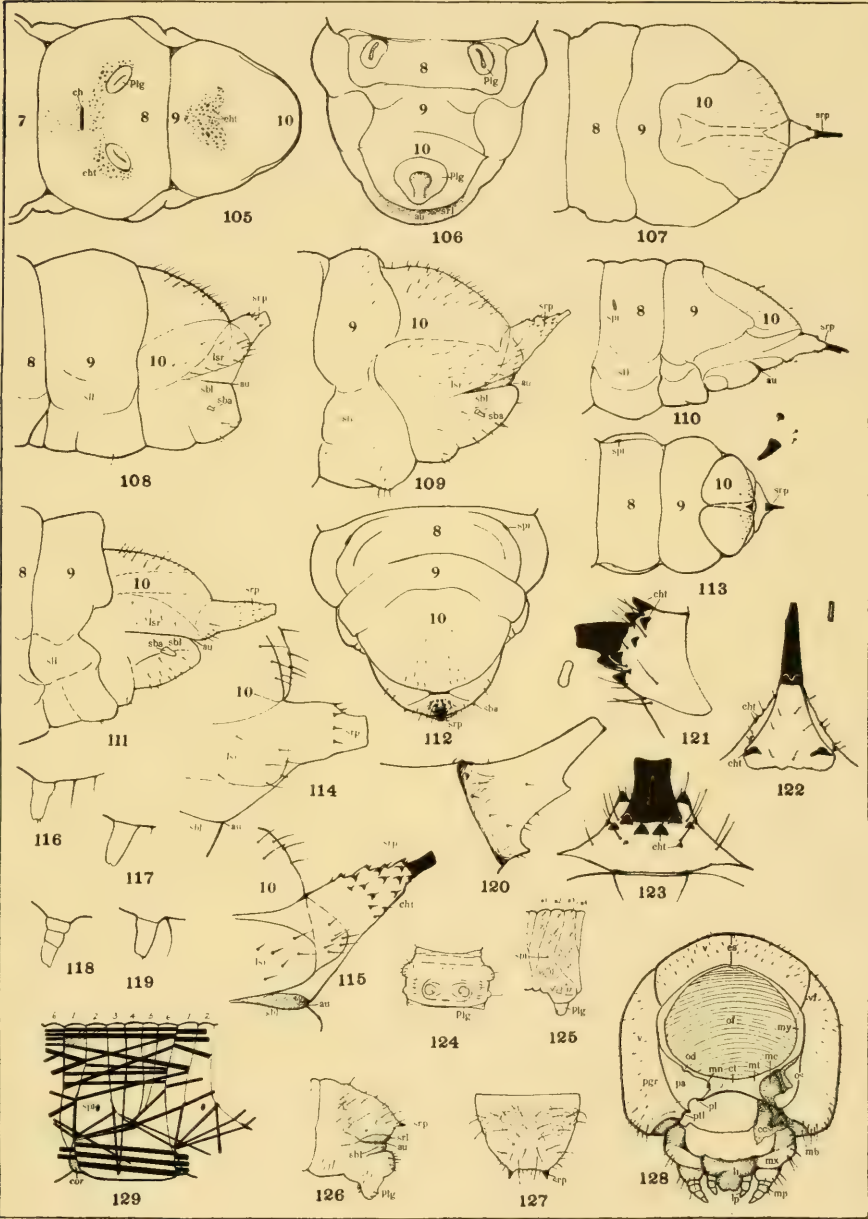
Fig. 127—*Pteronidea ribesi*. Dorsal aspect of caudal end of abdomen.

Fig. 128—*Abia americana*. Caudal aspect of the head.

Fig. 129—*Neodiprion lecontei*. Musculature of third abdominal segment. semidiagrammatic. Annulets numbered.

*au* anus  
*cc* cervacoria  
*ch* chitinized area  
*cht* chitinized tubercle  
*cor* coria  
*ct* corpotentorium  
*es* epicranial stem  
*li* labium  
*lp* labial palpus  
*lsr* lateral area of suranal lobe  
*mb* mandicoria  
*mc* maxacoria  
*mn* metatentorina  
*mp* maxillary palpus  
*mt* metatentorium  
*mx* maxilla

*my* maxillaria  
*od* odontoidea  
*of* occipital foramen  
*os* occipital suture  
*pa* postgena  
*pgr* postgenal ridge  
*pl* paracoila  
*plg* larvaped  
*pll* postcoila  
*pa* postgena  
*sba* subanal appendage  
*sbl* subanal lobe  
*sll* sublateral lobe  
*spi* abdominal spiracle  
*srp* suranal process





## PLATE XIII



## EXPLANATION OF PLATE

## ANTENNAE, LEGS, SILK-GLANDS

- Fig. 130—*Pamphilius* sp. Metathoracic leg.  
 Fig. 131—*Megaxyela major*. Metathoracic leg.  
 Fig. 132—*Macremphylus varianus*. Metathoracic leg.  
 Fig. 133—*Pteronidea ribesi*. Mesothoracic leg.  
 Fig. 134—*Neodiprion lecontei*. Metathoracic leg.  
 Fig. 135—*Dolerus similis*. Metathoracic leg.  
 Fig. 136—*Phlebotrophia mathesoni*. Metathoracic leg.  
 Fig. 137—*Metallus rubi*. Metathoracic leg.  
 Fig. 138—*Pteronidea ribesi*. Mesothoracic leg. Dorsal aspect.  
 Fig. 139—*Schizocerus zabriskei*. Metathoracic leg.  
 Fig. 140—*Kaliofenusa ulmi*. Metathoracic leg.  
 Fig. 141—*Caliroa cerasi*. Metathoracic leg.  
 Fig. 142—*Endelomyia aethiops*. Metathoracic leg.  
 Fig. 143—*Megaxyela major*. Antenna.  
 Fig. 144—*Adirus trimaculatus*. Antenna.  
 Fig. 145—*Schizocerus zabriskei*. Antenna.  
 Fig. 146—*Cephus pygmaeus*. Antenna.  
 Fig. 147—*Metallus rubi*. Antenna.  
 Fig. 148—*Tremex columba*. Antenna.  
 Fig. 149—*Kaliofenusa ulmi*. Antenna.  
 Fig. 150—*Phlebotrophia mathesoni*. Antenna.  
 Fig. 151—*Janus integer*. Antenna.  
 Fig. 152—*Hartigia cressoni*. Antenna.  
 Fig. 153—*Thrinax impressatus*. Antenna.  
 Fig. 154—*Pteronidea ribesi*. Antenna.  
 Fig. 155—*Tremex columba*. Mesothoracic spiracle.  
 Fig. 156—*Abia americana*. Silk-glands.  
 Fig. 157—*Abia americana*. Labium, hypopharynx, and portion of silk-glands, enlarged.  
 Fig. 158—*Abia americana*. Lateral aspect of cephalic portion of silk-glands.  
 Fig. 159—*Abia americana*. Dorsal view of silk-press, hypopharynx removed.  
 Fig. 160—*Abia americana*. Cephalic view of labium and hypopharynx.

a1-a6 antennal segments 1, 2, 3, 4, 5, and 6

an antacoria

crv cericos

cw tarsal claw

cx coxa

D arrow pointing dorsad

fm femur

fp femoral process

hx hypopharynx

li labium

lp labial palpus

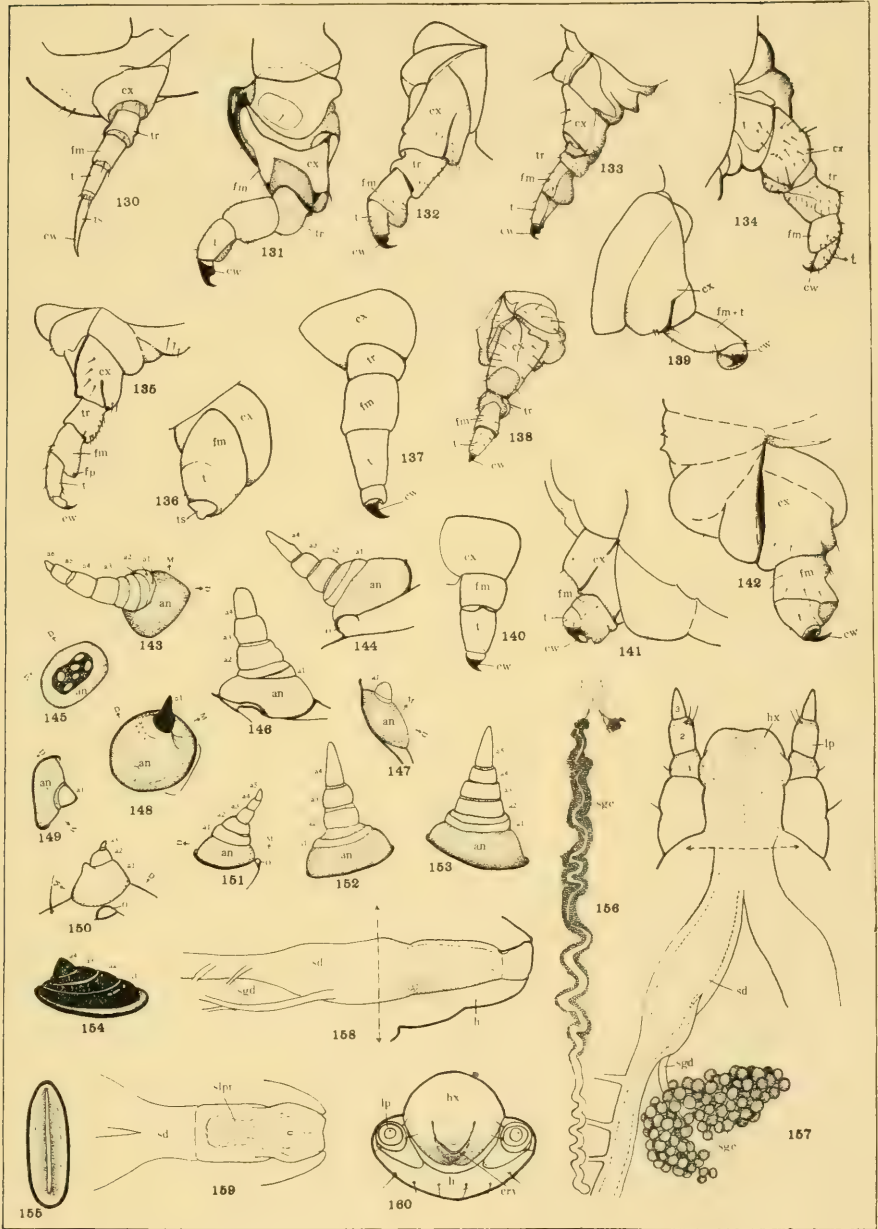
M arrow pointing mesad

sd duct of silk-glands

sgc cells of silk-gland

sgd small duct of silk-glands

slpr silk-press





## PLATE XIV



## EXPLANATION OF PLATE

Chart representing graphically the relationship of various taxonomic units or groups according to the more important modern systems of classification of the Tenthredinoidea as proposed by Konow (1905), MacGillivray (1906), and Rohwer (1911-1918).

MORE IMPORTANT MODERN SYSTEMS OF CLASSIFICATION OF THE TENTHREDINOIDEA		
KONOW 1905	MACGILLIVRAY 1906	ROHWER 1911-12
CHALASTOGASTRA	TENTHREDINOIDEA	CHALASTOGASTRA
<b>I. LYDIDAE</b> Lydini Megalodontides Lydides Cephini Xyelini Blasticotomini <b>II. SIRICIDAE</b> Xiphydrini Siricini Siricides Tremecides Oryssini <b>III. TENTHREDINIDAE</b> Cimbicini Cimbicides Abiides Syzygoniides Argini Argides Schizocerides Lophyrini Lobocerotides Pterygophorides Perreyides Lophyrides Tenthredinini Nematides Hoplocampides Blennocampides Selandriades Dolerides Tenthredines	<b>I. XYELIDAE</b> <b>II. PAMPHILIIDAE</b> <b>III. BLASTICOTOMIDAE</b> <b>IV. TENTHREDINIDAE</b> Diprioninae (1916) Emphytinae Selandriinae Dolerinae Phyllotominae Lycaotinae Tenthredininae Cimbicinae Hoplocampinae Dineurinae Monocteninae Cladiinae Nematinae Blennocampinae Fenusinae Scolioneurinae Hylotominae Schizocerinae Perreyiinae Incaliinae Lobocerinae Acordulecerinae Pterygophorinae Perginae <b>V. XIPHYDRIDAE</b> <b>VI. SIRICIDAE</b> Siricinae Tremecinae <b>VII. MEGALODONTIDAE</b> <b>VIII. CEPHIDAE</b> <b>IX. ORYSSIDAE</b>	<b>MEGALODONTOIDEA</b> <b>MEGALODONTIDAE</b> Megalodontinae Pamphiliinae <b>XYELIDAE</b> <b>CEPHIDAE</b> <b>ORYSSOIDEA = IDIO-</b> <b>ORYSSIDAE</b> <b>SIRECOIDEA</b> <b>XIPHYDRIDAE</b> Xiphidriinae Derecystinae <b>SIRECIDAE</b> Sirecinae Sirecini Xerini Tremecinae <b>TENTHREDINOIDEA</b> <b>CIMBECIDAE</b> Cimbecinae Cimbecini Phenacopergini Zaraeinae Pseudoclavellariini Zaraeini <b>PERREYIIDAE</b> Perreyiinae Philomastiginae <b>ARGIDAE</b> Arginae Sterichphorinae <b>BLASTICOTOMIDAE</b> <b>TENTHREDINIDAE</b> Diprioninae (1918) Allantinae Taxonini Eriocampini Allantini Dolerinae Tenthredininae Perineurini Tenthredinini Messinae Phyllotomini Pergini Athaliinae Emphytinae Lycaotini Blennocampini Phymatocerinae Selandriinae Selandriini Stenogasterini Cladiinae Nematinae Nematini Hemichlorini (1919) <b>PTERYGOPHORIDAE</b> Pterygophorinae Acordulecerinae (2) Phylactophaginae Euriinae (2) <b>PERGIDAE</b> <b>LOBOCERIDAE</b>



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Vol. VII

January, 1922

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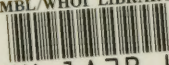








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